

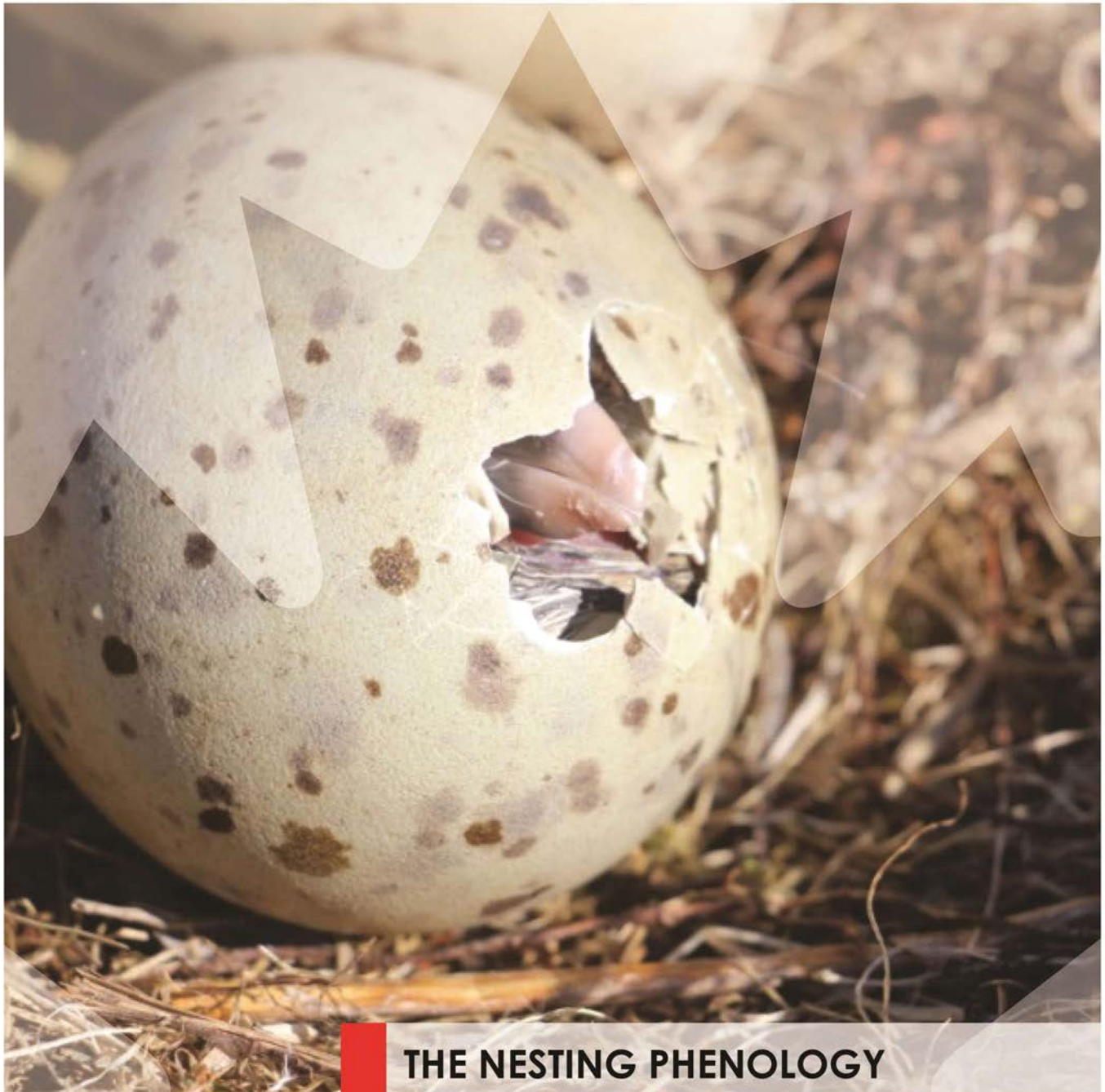


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THE NESTING PHENOLOGY OF BIRDS IN CANADA

FRANÇOIS ROUSSEU AND BRUNO DROLET
QUÉBEC REGION

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THE NESTING PHENOLOGY OF BIRDS IN CANADA

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All persons must adhere to the pertinent laws (e.g., provincial or territorial laws), regulations and permit requirements including, but not restricted to, the MBCA and the MBR. It is important to note that some bird species are protected under the MBCA and are also listed in Schedule 1 of SARA, and these species receive protection from both legislations.

The information within this document does not provide an authorization for the harming or killing of migratory birds or for the disturbance, destruction or taking of nests or eggs as prohibited under the MBR. It also does not provide a guarantee that a given activity will avoid contravening the MBR, or other laws and regulations.

It is the full responsibility of each individual or company to assess the risk of planned activities with regards to migratory birds, and to develop relevant avoidance and mitigation measures (see www.ec.gc.ca/paom-itmb). Since the nesting periods outlined in this technical report apply to large geographic areas, it is possible that the nesting period for a given species in a given location could have a different start date and/or duration than those published in this report. This may be due to micro-climatic conditions in specific areas (e.g., high elevation or coastal sites), and to inter-annual variation due to factors such as an early spring or a cold, wet summer. As it is possible that birds may nest before and/or after the nesting periods published in this report, the probability of encountering active nests outside the established nesting periods is much lower, but not null.

ABSTRACT

This technical report is the first attempt to produce a nationally consistent and unified description of bird nesting phenology across the different provinces and territories of Canada. It provides species-specific predictions of the nesting phenology of 311 bird species (71 % of those breeding in Canada), outlining the timing and intensity of nesting. The use of a standardized method applied to all regions enables predictions to be made for boreal and Arctic regions.

The first objective was to program a set of algorithms that would automatically process the hundreds of thousands of field observations contained in the nests records within the Project NestWatch database (Bird Studies Canada). A procedure was developed to reconstruct the most likely nest chronology with the greatest possible accuracy. The nest chronology was considered to start with the laying of the first egg and to end with the departure of the last young from the nest. The backcalculation algorithms were applied to 85% of the original nest records ($n = 202,407$), representing 478,419 nest visits.

The second objective was to make use of the estimated nest chronologies to develop models that would predict the nesting phenology of birds across Canada. The mean annual temperature (MAT) was the main predictor variable for the timing of nesting. The slope of the relationship between the MAT and nesting phenology was determined by the migratory strategy, the tendency to breed early or late, and the capacity to lay multiple clutches, while the intercept (or height) of prediction curves was determined by species. Quantile regression was used to describe the beginning, the midpoint and the end of the nesting period for each species. Predictions were derived from the three models and were restricted to the range of MAT experienced by a species within its normal breeding distribution. For most species, model predictions supported the two main initial assumptions, namely that the beginning of the nesting season should be earlier in warmer regions and that the length of the nesting season should be equal or progressively shorter with decreasing temperature. The coding for the backcalculation algorithms is available through the Internet as a package of R-language functions, named *rNest*.

The third objective was to determine whether the use of the backcalculation procedure was justified and whether it leads to biases when predicting nesting phenology, and to provide estimates of uncertainty concerning the predictions. In general, the bias in predictions associated

with using backcalculation was small for most species, and negligible compared to the uncertainty in the nesting phenology predictions, even for those species with a long active nest period. For a given species, the variable amount of nest records between regions, the quality of data and the constraints associated with the method used, coupled with the variability in the timing of nesting events between regions, individuals and years, contributed to different levels of uncertainty in the estimations. For several MAT intervals, there were sufficient nest records to allow satisfactory predictions of the nesting phenology based on local observations, but for other MAT intervals, the uncertainty around predictions was probably higher due to the fact that fewer data were available. In general, the uncertainty surrounding the estimated nesting dates can vary by up to about 10 days, or perhaps more in certain cases, due to natural variability in the timing of nesting events between regions, individuals and years.

The fourth objective was to consolidate the results of the first two objectives within a multi-species analysis to propose regional nesting calendars that would help determine regionally relevant periods during which nesting is likely to occur, and to provide a general portrait of the nesting phenology of federally protected bird species across Canada. To describe the general nesting period of migratory birds in a given region, the proportion of species actively nesting was calculated for each day from early March to the end of August. The regional nesting calendars were associated with broad geographical areas distributed across Canada, referred to as nesting zones.

The fifth and final objective was to provide a compendium of all the information that was used for, and generated by, the analysis of the Project NestWatch database. This is presented in the form of species-specific accounts. The aim of these is to provide easy access to practical information allowing a rapid assessment of the amount and quality of basic nesting information that was available for a particular species of interest, together with estimations of the nesting periods proposed for that species, and the uncertainty surrounding the predictions. The nesting period estimates for each species and for each of the 1,021 ecodistricts are available on the Bird Studies Canada website as an interactive on-line tool that offers the possibility of creating customized nesting calendars by selecting species and regions of interest.

RÉSUMÉ

Le présent rapport technique est la première tentative de description unifiée de la phénologie de nidification des oiseaux couvrant l'ensemble des provinces et territoires du Canada. Elle fournit des prédictions par espèce de la phénologie de nidification de 311 espèces d'oiseaux (71 % des espèces nichant au Canada), en décrivant leurs périodes et intensités de nidification. Des prédictions ont pu être établies pour les régions boréales et arctiques grâce à une méthode normalisée qui a été appliquée à l'ensemble des régions.

Le premier objectif était de programmer un ensemble d'algorithmes capable de traiter automatiquement les centaines de milliers d'observations de terrain contenues dans les relevés de nids consignés dans la base de données du Programme de suivi des nids d'oiseaux (*Project NestWatch*, Études d'Oiseaux Canada). Une procédure a été établie pour reconstruire la chronologie la plus probable pour chaque nid avec la plus grande exactitude possible. Nous avons considéré que la chronologie d'un nid débutait avec la ponte du premier œuf et se terminait avec le départ du nid du dernier jeune. Les algorithmes de rétrocalcul ont été appliqués à 85 % des relevés de nids originaux ($n = 202\,407$), qui totalisaient 478 419 visites de nids.

Le deuxième objectif était d'utiliser les chronologies de nid estimées pour élaborer des modèles permettant de prédire la phénologie de nidification des oiseaux dans l'ensemble du Canada. La température moyenne annuelle (TMA) était la principale variable prédictive pour la période de nidification. La pente de la relation entre la TMA et la phénologie de nidification était déterminée par la stratégie migratoire, la tendance à nicher hâtivement ou tardivement et la capacité de pondre plus d'une couvée, tandis que l'ordonnée à l'origine (ou la hauteur sur l'axe des y) des courbes de prédiction était déterminée par l'espèce. La régression quantile a été utilisée pour définir le début, le milieu et la fin de la période de nidification pour chaque espèce. Les prédictions ont été tirées de ces trois modèles et limitées à la plage de TMA à laquelle se trouve exposée l'espèce concernée dans son aire de reproduction normale. Pour la plupart des espèces, les prédictions des modèles vont dans le sens des deux principales prémisses de départ, à savoir que la période de nidification devait débuter plus tôt dans les régions plus chaudes, et que la durée de la période de nidification devait demeurer la même ou décroître progressivement avec la diminution des températures. La codification des algorithmes de rétrocalcul est disponible sur Internet sous la forme d'une suite de fonctions en langage R, nommée *rNid*.

Le troisième objectif était de déterminer si l'utilisation de la procédure de rétrocalcul était justifiable et si elle introduisait des biais dans la prédiction de la phénologie de nidification, ainsi que de fournir des estimations de l'incertitude concernant les prédictions. En général, le biais introduit dans les prédictions par le rétrocalcul était faible pour la plupart des espèces, et négligeable comparativement à l'incertitude dans les prédictions des phénologies de nidification, même pour les espèces chez lesquelles la période active de nidification est longue. Pour une espèce donnée, le nombre variable de relevés de nids entre régions, la qualité des données et les contraintes associées à la méthode utilisée, couplés à la variabilité des dates des événements de nidification entre régions, individus et années, contribuent à faire en sorte que les estimations présentent des niveaux variables d'incertitude. Pour plusieurs intervalles de TMA, le nombre de relevés de nids était suffisant pour permettre des prédictions satisfaisantes des phénologies de nidification fondées sur les observations locales, mais pour d'autres intervalles de TMA, l'incertitude des prédictions était probablement plus élevée en raison de la plus faible quantité de données disponibles. En général, l'incertitude entourant les dates de nidification estimées peut varier d'une période allant jusqu'à 10 jours, ou peut-être plus dans certains cas, en raison de la variabilité naturelle de la chronologie des événements de nidification entre régions, individus et années, et de l'échantillonnage et des contraintes associées à la méthode utilisée.

Le quatrième objectif était de réunir les résultats des deux premiers objectifs dans une analyse plurispécifique pour proposer des calendriers de nidification régionaux pouvant aider à déterminer, par région, les périodes où il est probable qu'il y ait nidification, et pour donner un portrait général de la phénologie de nidification des espèces d'oiseaux protégées au niveau fédéral dans l'ensemble du Canada. Pour décrire la période générale de nidification des oiseaux migrateurs dans une région donnée, la proportion d'espèces en nidification active a été calculée pour chaque jour du début de mars à la fin d'août. Les calendriers de nidification régionaux ont été associés à de vastes aires géographiques réparties dans l'ensemble du Canada, appelées zones de nidification.

Enfin, le cinquième objectif était de fournir un recueil de toute l'information utilisée ou produite dans le cadre de l'analyse de la base de données du Programme de suivi des nids d'oiseaux. Ce recueil est présenté sous la forme de comptes rendus sur les espèces. Nous voulions ainsi offrir un accès facile et pratique à cette information de façon à ce que toutes les personnes intéressées

puissent évaluer la quantité et la qualité de l'information de base sur la nidification qui était disponible pour telle ou telle espèce, ainsi que les estimations des périodes de nidification proposées pour l'espèce et l'incertitude entourant les prédictions. Les estimations des périodes de nidification pour chaque espèce et pour chacun des 1021 écodistricts sont disponibles sur le site Internet d'Études d'Oiseaux Canada sous la forme d'un outil interactif offrant la possibilité de créer des calendriers de nidification personnalisés en sélectionnant des espèces et des régions d'intérêts.

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GLOSSARY

Active period: The period when a nest is considered active. That is, the period from the laying of the first egg to the departure of the last young from the nest. The nest building period and the period of dependence of young outside the nest are excluded from the definition used in this report.

Actively nesting species: A species is considered to be actively nesting from the moment when 10% of the nests have been initiated (i.e., after the first egg has been laid), up until the moment when 90% of the nests have been vacated (i.e., after the departure of the last young).

BCR - Bird conservation region: An ecologically distinct region in North America as defined by the North American Bird Conservation Initiative, with similar bird communities, habitats, and resource management issues.

ESE: Expected standard error.

Extrapolation area: An area of possibly higher uncertainty in terms of prediction, where the minimum amount of data needed to reach a certain level of confidence in the predictions for a species was not available. Such areas were established using the relation between standard error and sample size. Greater caution is advised when using predictions within these areas. However, predictions in the extrapolation area do not necessarily differ from the “true” dates.

First egg date: The date on which the first egg is laid.

Interpolation area: An area of higher certainty in terms of prediction, where the minimum amount of data needed to reach a certain level of confidence in the predictions for a species was available. Such areas were established using the relation between standard error and sample size.

MAT: The mean annual temperature.

Migratory bird: A federally protected bird included under Article I of the Migratory Bird Convention and representing 83% of the nesting species in Canada.

Nest chronology: The set of dates during which a nest is active, as described by the nesting events of a nest record.

Nest departure date: The date of departure of the last young from the nest, which could be

close to the fledging stage for altricial species, or earlier for nidifugous or precocial species.

Nest observation: Observations made during a visit to a given nest (on a particular date).

Nest record: A record associated with one or more dates holding all observations made during visits to a nest.

Nesting event: Any of the events in the nesting process that can be described as happening at a more or less specific time, namely: the laying of the first egg, start of incubation, hatching, start of rearing, and departure of the last young from the nest.

Nesting phenology: The description of the variation in the timing of nesting of a given species of bird, or for several species of birds.

Nesting stage codes: The codes used by the *rNest* package to classify nest observations, namely: nest, laying, incubation, eggs, hatch, young, fledge, active, unknown (see Part 1 — Table 1.2 for full descriptions).

Nesting stages: The stages which comprise the period when a nest is active, namely: laying, incubation and rearing of young in the nest.

Nesting zones: The 27 geographical areas distributed across Canada that were determined by classifying ecodistricts according to variation in bird species assemblages, mean annual temperature and similarities in nesting phenology.

Precocial: Describes a bird species for which the rearing period inside the nest is approximately 24 hours.

rNest: A package developed in the R language enabling the backcalculation of nest chronologies from nest observations and the description of nesting phenology based on nest records (Rousseau and Drolet, 2017a).

Status codes: Codes used in Project NestWatch (Bird Studies Canada) to describe nest observations (see Part 1 — Table 1.1 for the description of the codes that were used in this report).

Theoretical chronology: A nesting period with a length determined by the nesting parameters recorded in the scientific literature.

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(Photo: Nest and eggs of Savannah Sparrow; F. Rousseu)

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(Photo: Nest and eggs of Common Eider; B. Drolet)

GENERAL INTRODUCTION AND OBJECTIVES

The nesting period is a vital moment in the annual cycle of birds. This is because they lay eggs and so for *a time* are highly vulnerable to multiple forms of disturbance. For example, the nest and/or the eggs of a bird can be inadvertently disturbed, damaged or destroyed as a result of diverse human activities, and the impact of this can have long-term negative consequences for bird populations in Canada, especially when considered in concert with the cumulative effects of other disturbances or causes of death that can affect birds (EC, 2015a, Calvert *et al.*, 2013). It is therefore not surprising that strict protection of nests and eggs has been identified as a priority for bird conservation since the signing of the *Migratory Birds Convention* 100 years ago, and that this has been integrated into Canada's legal framework for conservation, notably the *Migratory Birds Convention Act, 1994* and the *Migratory Birds Regulations*. If effective nest and egg protection is to be implemented, it is essential to know *when* birds are nesting. To be most useful, this information needs to be adapted to the greatest possible extent for a given region, taking into account local bioclimatic conditions, field realities (e.g., habitat or available nesting sites), and the bird species likely to be encountered. Although, basic biological information is available in the scientific literature for certain species or regions, it is not available for the whole of Canada in a common format. Therefore, the goal of this technical report was to provide a nationally consolidated picture outlining the timing and intensity of nesting for all regions of Canada, and for both single and multiple species. However, for many regions of Canada (especially those in the north) there are few nest observations that can be used to derive an accurate description of the nesting period based solely on locally obtained data. Therefore, to provide a meaningful portrait of the nesting season across the different regions, it was necessary to develop a method within a single framework that could adequately describe the nesting phenology of birds breeding in Canada.

The present study had five objectives:

- The first objective (Chapter 1) was to use the hundreds of thousands of field observations (nests records) in the Project NestWatch database (BSC, 2013) to derive information on nesting phenology. The second and third objectives (Chapters 2 and 3) were to make use of the estimated nest chronologies to develop models that would predict the nesting phenology of birds across Canada, and to estimate the possible biases and

uncertainty of these models. Because most of the available nest records were concentrated in the south, and were dominated by more common or easily observed species (e.g., American Robin, Tree Swallow and Red-winged Blackbird¹), two important challenges were to estimate the nesting phenology of species with few nest observations and of species outside those regions with abundant data. This predictive analysis also provided an opportunity to assess two important aspects. The first of these was to determine whether the use of the backcalculation procedure was justified and whether this leads to biases when predicting nesting phenology and the second was to provide estimates of uncertainty concerning the predictions.

- The fourth objective (Chapter 4) was to consolidate the results of the first two objectives within a multi-species analysis that would produce nesting calendars for migratory birds that would help determine regionally relevant periods during which nesting is likely to occur, and to provide a nationally consistent general portrait of the nesting phenology of federally protected bird species.
- The fifth objective (Part 2 – *Species Accounts*) was to provide a compendium in the form of species-specific accounts containing all the information that was used for and generated by the analysis of the Project NestWatch database. The idea being to provide quick and easy access to all the information, so that anyone interested can assess the amount and quality of basic nesting information that is available for a particular species of interest, and the estimations of the nesting periods proposed for that species, along with the uncertainty surrounding the predictions.

The present study was inspired by the innovative work of Peck *et al.* (2007), who proposed core nesting periods based on data from the Ontario Nest Records Scheme; of Gauthier and Aubry (1995), who proposed species-specific nesting calendars based mainly on data from the Québec Nest Records Scheme; and of Peck and James (1983), who proposed an account of the nidiology of the birds of Ontario.

¹The scientific names of all the bird species mentioned in this report are provided in Part 2 – *Species Accounts*.

PART 1: DETERMINING NESTING PHENOLOGY

CHAPTER 1: ESTIMATING NEST CHRONOLOGY

1.1 Introduction

Any event in the nesting process that can be linked to a specific date can be used to estimate the *nest chronology*, which is the set of dates during which a nest is active. Typically, the use of raw data collected by ornithologists during visits to nests requires a high number of observations to provide an adequate picture of the nesting activity of a given species. Furthermore, relying solely on the raw information (without the use of backcalculation algorithms) to determine the active nesting period, may underestimate its duration. The latter is especially true if few nest observations are available, which it is often the case for rare or elusive species, or for species at risk (see Chapter 3 concerning the biases and uncertainties associated with the use of raw or backcalculation data).

For the present study, the raw data from the nest observations available were used to estimate the period when a nest was active (i.e., the period between the laying of the first egg and the departure of the last young from the nest). The nest construction period was not considered in the study because its length can vary greatly between individuals and under different conditions (e.g., the reuse of a previously constructed nest or the building of a new one, and possible delays of different lengths between nest completion and the laying of the first egg). Moreover, observations of nest construction are difficult to consider in a backcalculation procedure because birds can show nest construction behaviour before and after laying, and during the rearing of young. The pre-laying period (e.g., pairing and the selection of a nesting site) and the post departure period (i.e., the rearing period outside the nest) were also not considered, as they cover periods when the nest is not in use. These nesting stages more closely concern adults and juveniles than broods.

For a given nest, the objective was to reconstruct the most likely nest chronology with the greatest possible accuracy, using all the pertinent information available. Because most nests were only visited once (approximately 50% of nest records in the Project NestWatch database (BSC, 2013)), there was substantial inherent uncertainty in the estimation of the nest chronology. However, for nest records with more than one observation, an effort was made to use the

information in backcalculations to obtain the most probable chronology. One important consideration with the approach used was to be able to provide estimates of uncertainty associated with each backcalculated nest chronology.

Another important guiding principle during the development of the backcalculation algorithms was that the inferred nest chronologies should never contradict the data recorded in the nest records. To achieve this, observations that were indicative of transitions between nesting stages (i.e., laying, incubation and rearing) were identified to be used as end points for the different stages of the nesting period. This implies that the nesting parameters for a given species, such as the length of the rearing period, were modified according to the observations to ensure that the inferred nest chronology never contradicted the observations. Thus, when it could be inferred from the data available that the lengths of the different nesting stages differed from the range of values described in the literature, the estimated nest chronology was adapted to take the former data into account. Otherwise, it was assumed that the nesting stages of the observations were in accordance with the range of values of the nesting parameter given in the literature, and these were used to infer nest chronology.

The backcalculation algorithms were developed as an interactive tool using R (R Development Core Team, 2010), a language and environment for statistical computing and graphics. R is distributed as an open source and the software is available free of charge under the Free Software Foundation's General Public License (GNU). The tool is currently assembled as an R package, entitled *rNest*, which comprises several functions and a user interface allowing the nest chronology and nesting phenology to be estimated. This package, which was designed for general use, is now in the public domain (Rousseu and Drolet, 2017a).

Once nest chronologies have been estimated for a set of nests for a given species, all chronologies can then be compared and studied based on the same suite of nesting events, and the nesting phenology for a species can also be modelled (see Chapter 2).

1.2 Nest records

Over 99% of the nest records used in this study come from the Project NestWatch database (238,127 nest records containing 638,381 nest observations or visits (BSC, 2013)). The dataset was completed with information from two other data sources providing records from the

Checklist Program of the Northwest Territories (1,478 records; EC, 2014) and from a study on bird nesting phenology in Nunavut (728 records; Coulton and Robertson, 2009). Both these datasets provided a single observation for each nest record. The dataset for the Northwest Territories had observations with the mention of either eggs or young of unknown number in the nest, while the Nunavut dataset provided additional information that could be used to identify the dates for the first egg, incubation, hatching, rearing or departure of young from the nest.

Project NestWatch is a national program coordinated by Bird Studies Canada, and also incorporates provincial and regional nest record schemes that focus on the long-term monitoring of nesting activity of birds across Canada. It relies on nest observations gathered by volunteers and various other participants willing to contribute their data to the database, including British Columbia Nature, Alberta Nature, the Royal Saskatchewan Museum, the Manitoba Museum, the Royal Ontario Museum, the Canadian Museum of Nature (for Québec), and the Canadian Wildlife Service – Atlantic Region (for the Maritimes). Breeding bird atlases also contribute data from nest monitoring forms to the program.

Nest record schemes were initiated in Canada in the mid-1950s and were based on the method developed by the British Trust for Ornithology in 1939. The aim of these schemes was to obtain standardized nesting data for birds. Bird Studies Canada launched Project NestWatch in 2002 to increase the collection of nesting data and to provide a repository for all nest record scheme databases in Canada. Data for Project NestWatch were originally submitted on cards but, after a gradual transition period, these are now all submitted online. For this study, a huge nation-wide effort was made to computerize as many nest record cards as possible. Given the size of the database, there was no systematic validation for inaccurate nest observations or for data entry errors, except in the case of the *Fichier de nidification des oiseaux du Québec*.

The vast majority of the nests in Project NestWatch were observed in or around populated areas in the southern part of Canada (Figure 1.1). Although the earliest nest records date back to the 19th century, over 90% were collected between the mid-20th century and 2013 (Figure 1.2), and over 50% between 1966 and 1986. The latter period corresponds to intensive surveys done for breeding atlases in Ontario and Québec. In terms of diversity, the nest records considered ($n = 202,407$) provide data for 335 (76%) of the 439 bird species known to nest in Canada (EC, 2015b), and cover 76% of federally protected species and 68% of non-federal species. The ten

most commonly recorded species (more than 3,000 records/species) account for just over one third of all nest observations. The first 10% were for the American Robin ($n = 20,241$); the following 11% were for the Tree Swallow ($n = 11,761$) and Barn Swallow ($n = 10,439$); and the following 14% were for the Red-winged Blackbird ($n = 6,019$), Song Sparrow ($n = 4,599$), Yellow Warbler ($n = 3,940$), Mountain Bluebird ($n = 3,894$), Cedar Waxwing ($n = 3,469$), Eastern Kingbird ($n = 3,373$) and Killdeer ($n = 3,181$). The next 38 species had between 1000 and 3000 nest records (32%), followed by 245 species with between 30 and 999 records (33%), followed by 42 species with between 10 and 29 records (0.4%), and finally, 103 species with less than ten usable nest records.

1.3 Backcalculation information

The nesting events that were used to estimate the nest chronology of a given nest were inferred using three basic pieces of information: 1) the dates of visits to a nest and the content of that nest (number or presence of eggs and/or young); 2) the description of nesting observations based on the status codes used in Project NestWatch; and 3) the nesting parameters for the species within the scientific literature. The geographical coordinates of the nest were also used to describe the nesting phenology of a given region.

For certain species, it is difficult or impossible to examine the nest contents (e.g., for cavity nesters or when nests are out of reach). However, while the exact content of a nest may be impossible to determine (i.e., whether it contains either eggs, young or both), a nest can still be considered active based on the observation of behaviour confirming the presence of an active nest. We therefore also used the observations of active nests in the backcalculations, although this type of information tends to provide less precise estimates.

Nesting codes

The status codes employed by Project NestWatch were used to provide additional information about the state of a given nest, particularly regarding nest construction, egg laying, incubation, hatching and fledging (Table 1.1), thus giving a more accurate backcalculation estimate. Nest records only reporting observations indicative of nest construction were discarded.

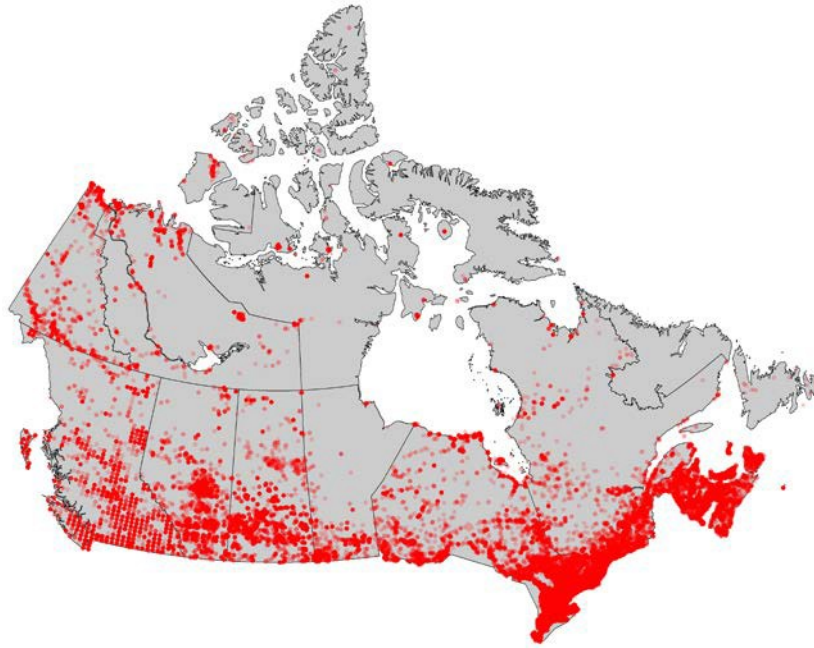


Figure 1.1. Location of nest records used in the current study. Most nests (>99%) come from the Project NestWatch database (BSC, 2013). Points are plotted with transparency to provide a better idea of the density of nest records across regions.

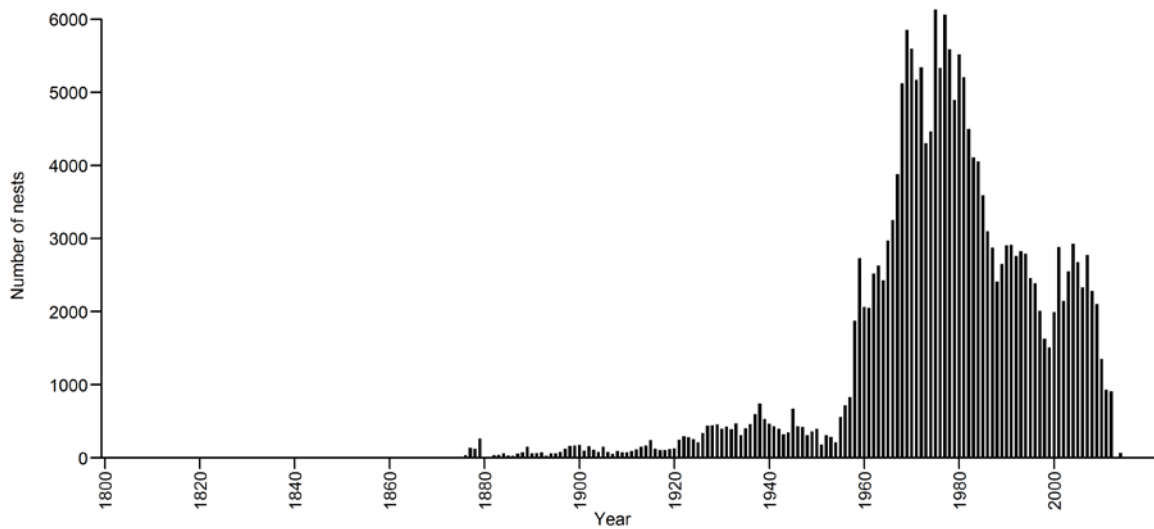


Figure 1.2. Temporal distribution (from 1800 to 2013) of nest records used in the current study. Most nests (>99%) come from the Project NestWatch database (BSC, 2013).

Table 1.1. Project NestWatch status codes used to classify nest observations into the nesting stages employed in the backcalculation procedure to estimate nest chronologies

Status code	Description	Nesting stages
AB / FB / MB / PB	Adult / female / male / pair carrying nest material	Nest
N1 / N2 /N3	Nest one quarter / half / three quarters built	Nest
N4 / NC	Nest completed but unlined	Nest
NL	Nest completed and lined	Nest
FR	Egg freshly laid (i.e., assumed to have been laid on the day of observation). Depending on the number of eggs, this could cause the observation to be classified either in the laying or the incubation stage.	Laying or incubation
HA	Hatching	Hatching (start of rearing)
PI	Pipping or calling from egg	Hatching (start of rearing)
RF	Young ready to fledge	Nest departure (end of rearing)
SL	Young seen leaving the nest naturally	Nest departure (end of rearing)
SY	Some young fledged, other live young still in nest	Nest departure (end of rearing)
YC	Young capable of leaving nest on previous visit	Nest departure (end of rearing)
LB	Young left naturally before fledging	Nest departure (end of rearing)
ON	Young outside underground nest or burrow	Nest departure (end of rearing)
EX	Young “exploded” from nest when inspected	Nest departure (end of rearing)

Nesting parameters

Except for clutch size, the nesting parameters used (subsequently considered as theoretical parameters) were largely those compiled by Denis Lepage (Bird Studies Canada) using the *Life Histories of North American Birds* (Bent, 1919-1968). Certain theoretical parameters were also obtained from the online version of *The Birds of North America* (2015). In a few cases, species with missing data were given the same parameters as very similar or closely related species. The nest chronology for a given species was inferred using six nesting parameters: 1) the estimated clutch size; 2) the minimal clutch size above which a nest was assumed to have reached the incubation stage, and below which it was assumed to be in the laying stage; 3) the number of days between the laying of two consecutive eggs; 4) the number of eggs before the onset of incubation (i.e., at the first egg, the second and so on, or considered to be with the penultimate egg laid or the last egg); 5) the length in days of the incubation period; and 6) the length of the rearing stage in the nest. The minimal and the estimated clutch sizes were inferred from the data.

The proportion of nest visits during which a given number of eggs was counted, and the used clutch size, are shown for each species in Panel 1 of Part 2 – *Species Accounts*. In most cases, the clutch size used was the modal number of eggs but, when the distribution of clutch sizes had no clear modal value, a number was subjectively chosen among the most likely values. In cases where two eggs were laid over three days, the laying interval was considered to be one day. Nest records of species with precocial young were assumed to have a rearing stage (in the nest) of one day to allow for the presence of young in the nest for a period of 24 hours. Finally, the possibility of a delayed incubation, starting sometime after the laying of the last egg, was not considered.

1.4 Backcalculation procedure

Step 1: Determination of clutch size

The first step was to determine the maximal number of eggs and/or young observed to provide an estimate of the clutch size for a given nest. When eggs and young were present on the same date, the numbers of both were summed to obtain the maximal number of eggs possible. If the maximal number of eggs was observed during visits spanning a length of time greater than the laying interval; or if young were observed in the nest; or if at a given visit the number of eggs was equal or superior to the minimal clutch size, it was assumed that the clutch size could be inferred by using the maximal clutch size observed within the nest observations, and this number was used as the clutch size. If the maximal number of eggs recorded was observed during consecutive visits spanning a length of time inferior or equal to the laying interval, and if this number was inferior to the minimal clutch size, it was assumed that the maximal observed number of eggs and/or young was unrealistic, and the estimated clutch size was used to estimate the nest chronology instead. The estimated clutch size was also used when there was no information given concerning the number of eggs or young. (See Panel 3 of Part 2 – *Species Accounts* for the values of the nesting parameters used for each species.)

Step 2: Classification of observations

The second step for each nest was to classify each visit according to the ordered categories corresponding to the different possible nesting stage codes (Table 1.2). A given visit was only accorded a stage code that was equal or higher in order to the stage code given to the previous visit. For example, if there were two visits to a given nest and young and eggs were seen in the

nest during the first visit, but only eggs were seen during the second visit, the second visit could only be categorized as being in the “young”, “fledging” or “unknown” stage. This was to prevent confusion that could arise from inconsistent or difficult to interpret observations, such as when unhatched eggs remained in the nest during the rearing stage or once the young had left the nest. When several nest observations were made on the same date, the nest stage for that date was determined using the most advanced nesting stage code given by the algorithm.

In the case of observations for which only eggs were seen, *rNest* initially classified these with the stage code “eggs”. In the case of nests for which the number of eggs or young was known, observations at the “eggs” stage were further divided into “laying” or “incubation”, according to the procedure described below (see Step 3). When there was no information on the number of eggs, the stage code remained “eggs”. When there was no information on either the number of eggs or of young (i.e., -1, -1), it was assumed that eggs or young were present, but in unknown numbers. In such cases, the visit was given the nesting stage code “active”.

The stage codes “nest” and “fledging” could only be given if the observer had provided an appropriate status code for a given observation (Table 1.1). The stage code “hatch” could be given either when an appropriate status code was provided by the observer, or when the day of hatching could be inferred from the observations (see Step 4).

Once the stage code “unknown” was given, all following observations were also considered as “unknown” and ignored by *rNest* when estimating chronologies. No attempt was made to incorporate a procedure into the backcalculation to allow the detection of a second nesting event within the same nest. In such cases, if no visits were classified as “unknown”, it is possible that the estimated nest chronologies included both nesting attempts. However, such nests records were likely rejected for the modelling purposes when the length of their active period was compared with the theoretical length estimated using known nesting parameters (see Chapter 2). Because nest observations classified as “unknown” were ignored by *rNest*, the nest departure date was estimated independently of these visits, and could be estimated later than earlier visits reporting the absence of eggs or young.

Table 1.2. Conditions for the classification of nest observations using different nesting stage codes in relation to the number of eggs (n) and/or young (m) observed. Values of -1 indicate the occurrence of eggs and/or young of unknown number

Number or presence of eggs and/or young	Conditions	Nesting stage code
(0, 0)	No eggs or young observed and content of nest reported empty on all previous visits (if any).	Nest (unknown nesting stage)
(-1, 0); (n, 0)	Occurrence of unknown number of eggs (-1); or a number of eggs (n) reported in the nest.	Eggs (laying or incubation)
(-1, 0); (n, 0)	Occurrence (-1); or a number of eggs (n) reported in the nest with an increase in the number of eggs/young in following visits, but the number of eggs has not reached the minimal clutch size; or the number of eggs observed is below the number of eggs at which incubation starts.	Laying
(-1, 0); (n, 0)	Occurrence (-1); or a number of eggs (n) reported in the nest and a status code indicative of incubation is given with the observation; or the number of eggs observed is equal or higher than the number of eggs above which incubation starts, or has reached the inferred clutch size for the nest.	Incubation
(-1, 0); (0, -1); (-1, -1); (n, -1); (-1, m); (n, 0); (0, m); (n, m)	The first observation of young reported in the nest when an increase in the number of young (m) is detected in following visits, or the first report of a status code indicative of hatching	Hatch (first day of rearing)
(0, -1); (-1, -1); (n, -1); (-1, m); (0, m); (n, m)	Occurrence (-1); or a number of young (m) reported in the nest; or a status code indicative of hatching is used for that observation.	Young (rearing)
(0, -1); (-1, -1); (n, -1); (-1, m); (0, m); (n, m)	A status code indicative of nest departure (fledging) has to be given for an observation to receive this code.	Fledging (end of rearing)
(-1, -1)	Occurrence of an unknown number (-1) of eggs or young reported in nest.	Active (laying, incubation or rearing)
any values	This code was given when a nest was empty and previous visits were classified with a nesting stage code implying nesting activity (i.e., other than stage code “nest”), or when the number of young was 0 but where young were reported in previous visits. Once this code was given, all subsequent visits were classified with the same code despite the content of the nest.	Unknown

Step 3: Detection of laying

Laying is assumed to have occurred whenever there was an increase of the number of eggs reported between visits for observations classified in the nesting stage “eggs”, or when the number of eggs observed was below the minimal number of eggs at which incubation starts. When an observation featured the status code “egg fresh” (Table 1.1), it was assumed that an egg was laid on the day of observation. When laying was detected, the estimated clutch size and the onset of incubation for the species were used to infer the number of eggs at which incubation started. Once this number was reached or exceeded in the observations, the current and all subsequent visits with stage code “eggs” were assumed to be in the “incubation” stage, and previous observations with eggs were considered to be in the “laying” stage. This ensured that observations were correctly classified despite a potential decrease in the number of eggs after the start of incubation (e.g., due to partial predation, or the rejection of eggs by the Brown Cowbird).

Step 4: Detection of hatching

Hatching was inferred whenever there was an increase in the number of young between visits classified at stage code “young”. When an increase was detected, the first observation with stage code “young” was assumed to be the hatching date, which marks the first day of the rearing period. The first code indicative of hatching was also used to mark the beginning of the rearing period. The simultaneous presence of eggs and young could also have been interpreted as an indication of hatching. However, numerous reports of active nests in the Project NestWatch database could be interpreted as indicative of the presence of infertile or unhatched eggs, which seems to be relatively common in birds (Koenig, 1982). For this reason, a single observation of a nest containing both eggs and young without a code indicative of hatching was classified as being at stage code “young”.

Step 5A: Adjusting nesting parameters – laying

When no observations were classified in the “laying” stage, the laying sequence was reconstructed using the clutch size and the theoretical nesting parameters. For example, for a species laying 1 egg every other day and with a clutch size of 4, the theoretical laying sequence would be 1-1-2-2-3-3-4. When some observations had been made prior to the laying of the first egg and the nest was still empty, the laying sequence was reconstructed so as not to extend into

the period during which the nest was reported as empty.

When two or more observations were classified in the “laying” stage, *rNest* first tried to fit the theoretical laying sequence to the observations. If this sequence contradicted observations, the laying sequence was reconstructed using two steps: one that started from the first egg observation and reached the laying of the first egg; and one that completed the laying sequence up to the final clutch size. Again, the theoretical laying interval was used to reconstruct these two partial sequences. Because both partial sequences generally extended beyond the observations, they did not contradict the observed data. This allowed an atypical laying sequence for a given nest. However, for unobserved laying events, it was always assumed that the laying interval was the one implied by the theoretical nesting parameters of the species. Moreover, unless the clutch size was reached earlier than expected and some observations were from the “nest” stage, or eggs were laid at atypical intervals, the laying sequence was assumed to be inflexible when compared to incubation and rearing. In other words, unless observations implied otherwise, the laying sequence was never shortened in relation to the laying interval.

Step 5B: Adjusting nesting parameters – incubation and rearing

To estimate the length of the incubation and rearing periods, *rNest* scanned for any information that might require a modification of the nesting parameters. For example, when it could be inferred from the observations that the incubation period lasted longer than that given by the theoretical nesting parameters, the length of the incubation period assigned to the nest was modified to accommodate the observations. The same procedure was applied to the rearing period for altricial species. When the data indicated that a given period had been longer than the one suggested by the theoretical nesting parameters, it was assumed that it extended only as far as the data indicated. For example, if observations of young in the nest spanned 15 days and the length of the theoretical rearing period was 13 days, the former length was used to estimate the nest chronology. A given period could also be shortened if the data marked the beginning and end of the period. For example, if it was possible to determine the hatching and fledging dates from the observations, the period in between was considered to be the rearing period, even if it was shorter than the theoretical value.

When incubation and rearing observations spanned a number of days greater or lower than the

sum of the theoretical values for the length of incubation and rearing, the observations superseded the theoretical values. In such cases, the lengths of both periods were adjusted proportionally to their theoretical relative lengths.

Step 5C: Adjusting nesting parameters – unknown number of eggs or young

When eggs were known to be present during certain visits, but not their number, observations were left classified as stage code “eggs”. Moreover, if the number of young was also unknown, the estimated clutch size was used to estimate the nest chronology, and the length of the laying and the incubation periods were summed to adjust the estimated chronology to the observations of eggs. When a nest was only reported as being “active” on different dates, the length of the active period was determined by summing the lengths of the different theoretical nesting stages and comparing these to the observations. If nest observations spanned a number of days greater than that predicted from theoretical values, the inferred lengths of incubation and/or rearing were adjusted with the procedure described in Step 6, Case 3.

Step 6: Inferring first egg and nest departure dates

Each nest was classified based on all the usable information that allowed the most accurate chronology to be achieved. Nest chronologies were backcalculated under the following cases, which are listed in decreasing order of the expected level of certainty in the backcalculated dates obtained:

Case 1: When laying was detected

When laying was detected, the date of the first egg was backcalculated using the theoretical laying sequence. The incubation and rearing periods were then added to the laying sequence in accordance with the observations. If any observations marked the beginning or the end of the incubation or the rearing period, the nest chronology was adjusted to fit the observations. If there was a single observation classified in the laying stage, it was assumed that the most recent egg laid was laid either on the day it was observed (for a laying interval of 1 or 2 days) or on the previous day (for a laying interval of 3 days).

Case 2: When hatching AND/OR fledging or nest departure were detected

When hatching and/or fledging or nest departure had been detected, but not laying, the nest chronology was adjusted to fit these nesting events.

Case 3: When incubation AND rearing were detected

When there were observations classified in the incubation and the rearing stages, but no observations marked the beginning or the end of either stage, the incubation and the rearing sequences were fitted so that observations were as close to the middle of the theoretical chronology as possible. To do so, the algorithm minimized the difference of the ratios between the numbers of days before and after the observations (Figure 1.3). This approach eliminated the bias associated with other methods, such as centering all observations on their corresponding sequences. When there was a tie, the earliest nest chronology was chosen. This was deemed justifiable in terms of conservation because eggs are more vulnerable to possible disturbances to the nest than are young about to leave the nest, and selecting the earliest option ensures that the “egg” nesting stage is fully covered by the estimated nest chronology.

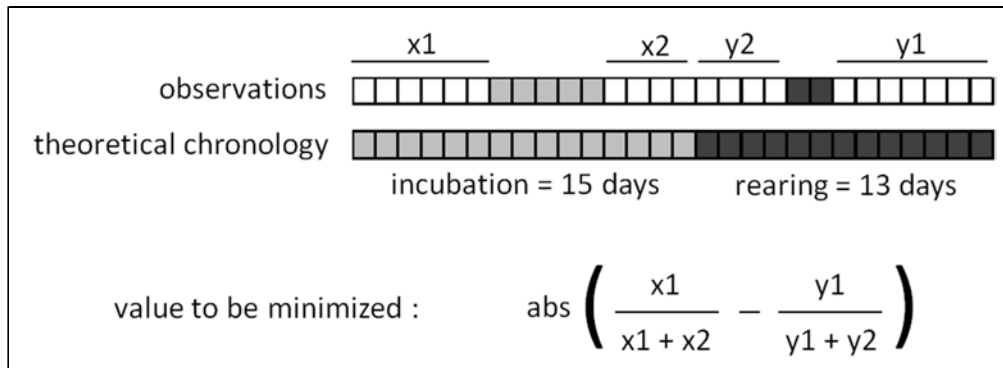


Figure 1.3. Method used for estimating the nest chronology when only incubation and rearing observations were available. Values are in numbers of days.

Case 4: When incubation OR rearing was detected

When observations were classified either in the “incubation” or “rearing” stage, the theoretical chronology was fitted so that the observations were placed in the middle of

the sequence. Again, when there were two possibilities, for conservation purposes, the one associated with the earliest first egg date was chosen.

Case 5: When only an unknown number of eggs was reported

When nest observations only reported an unknown number of eggs (with zero young), the laying and the incubation sequences were centered on the observations.

Case 6: When only nest activity had been detected

When all observations had been classified as “active”, the theoretical active period (from the laying of the first egg to the departure of young from the nest) was centered on the nest observations.

1.5 Estimating backcalculation uncertainty

For each nest, an estimate of the uncertainty associated with backcalculation was computed. This was based on the number of days during which the first egg could have been laid without the available observations contradicting the theoretical chronology fitted. For the calculation, it was assumed that the lengths of the different nesting stages were equal to their expected theoretical lengths (Figure 1.4). It was considered that there was no uncertainty for nests for which laying, hatching or fledging information was available, or for nests for which observations spanned the length of the theoretical nesting period. Although for many nest records, the actual length of certain stages differed from their expected theoretical lengths, this uncertainty was not incorporated, as it probably differs within and between species and would be difficult to quantify. The intention was more to provide an idea of the uncertainty in the estimation of the nest chronology, which could be used to quantify the relative quality of the information provided by different nest records. (See Section 2.3 for their use in modelling, and Chapter 3 for a discussion on uncertainties and biases associated with estimations.)

1.6 Examples of backcalculated nest chronologies

The figures 1.5 to 1.7 show different backcalculation results from the *rNest* package. The examples are arranged from the simplest case of a nest with a single observation, to more complex cases with multiple observations implying a variety of nesting stages and events. Examples were built using fictitious nesting parameters and different nesting stage codes.

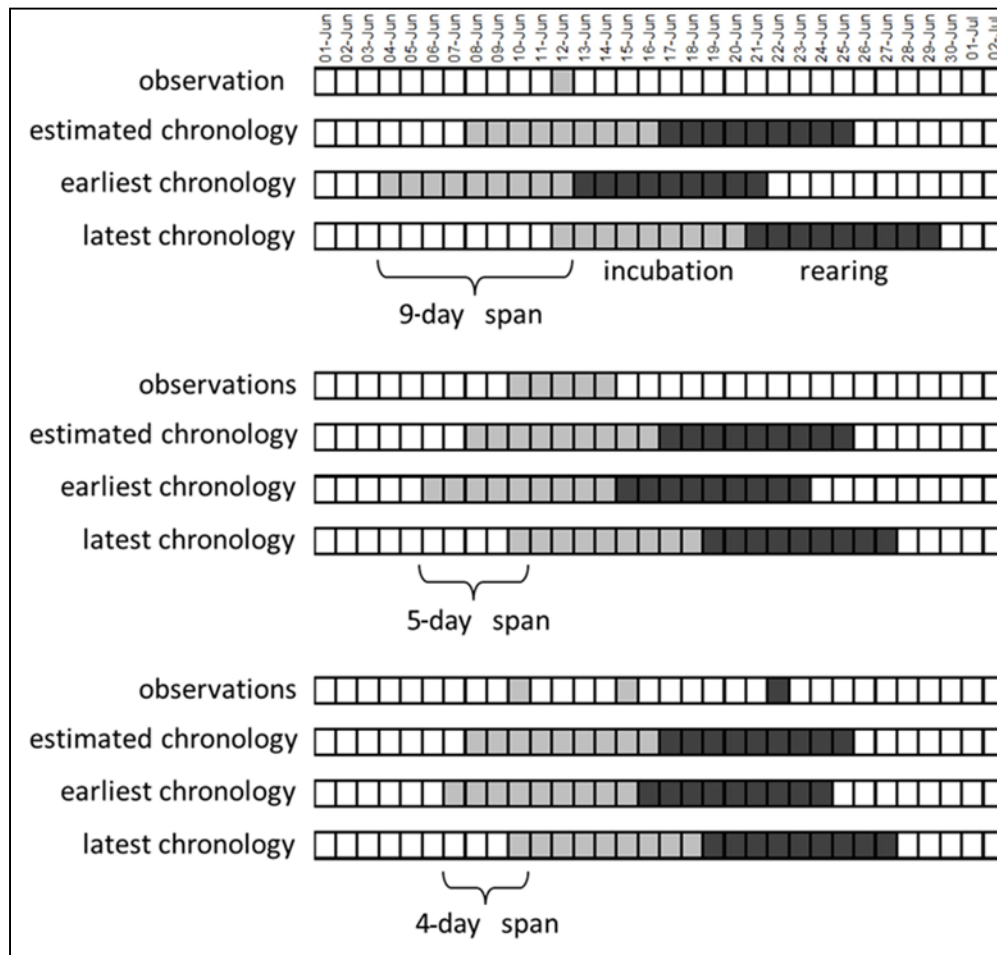


Figure 1.4. Examples of the method used to estimate the backcalculation uncertainty of three nest records with different nest observations. The backcalculation uncertainty was estimated by determining the number of days by which the chronology could be moved before or after the estimated chronology, without contradicting the nest observations.

Example 1					Example 2				
Date	Observation		Backcalculation		Date	Observation		Backcalculation	
	Egg	Young	Nesting stage code	Nest chronology		Egg	Young	Nesting stage code	Nest chronology
2000-04-26									
2000-04-27				Laying					
2000-04-28				Laying					
2000-04-29				Laying					Laying
2000-04-30				Incubation					Laying
2000-05-01				Incubation					Laying
2000-05-02				Incubation					Incubation
2000-05-03				Incubation					Incubation
2000-05-04				Incubation					Incubation
2000-05-05	4	0	Incubation	Incubation	-1			Egg	Incubation
2000-05-06				Incubation					Incubation
2000-05-07				Incubation					Incubation
2000-05-08				Incubation					Incubation
2000-05-09				Incubation					Incubation
2000-05-10				Young					Incubation
2000-05-11				Young					Incubation
2000-05-12				Young					Young
2000-05-13				Young					Young
2000-05-14				Young					Young
2000-05-15				Young					Young
2000-05-16				Young					Young
2000-05-17				Young					Young
2000-05-18				Young					Young
2000-05-19				Young					Young
2000-05-20				Young					Young
2000-05-21				Young					Young
2000-05-22									Young
2000-05-23									Young
2000-05-24									

Nesting parameters: estimated clutch size = 4 eggs; minimum clutch size = 3 eggs; maximum clutch size = 6 eggs; laying interval = 1 day; onset of incubation = with the last egg laid; length of incubation = 10 days; and length of rearing period = 12 days.

Example 1: Nest record reporting a number of eggs corresponding to the estimated clutch size. The observation was placed in the middle of the incubation stage.

Example 2: Nest record reporting an unknown number of eggs. The mean clutch size was used to construct the laying sequence and the observation was placed in the middle of the period with eggs.

Figure 1.5. Examples of fictitious nest records from the package *rNest* with a single observation (visit).

Example 3					Example 4				
Date	Observation		Backcalculation		Egg	Young	Backcalculation		
	Egg	Young	Nesting stage code	Nest chronology			Nesting stage code	Nest chronology	
2000-04-26				Laying					
2000-04-27				Laying					
2000-04-28				Laying				Laying	
2000-04-29				Incubation				Laying	
2000-04-30				Incubation				Laying	
2000-05-01				Incubation				Laying	
2000-05-02				Incubation				Laying	
2000-05-03				Incubation				Incubation	
2000-05-04				Incubation				Incubation	
2000-05-05	4	0	Incubation	Incubation	5	0	Laying	Laying	
2000-05-06				Incubation				Incubation	
2000-05-07				Incubation				Incubation	
2000-05-08				Incubation				Incubation	
2000-05-09				Young				Incubation	
2000-05-10				Young				Incubation	
2000-05-11				Young				Incubation	
2000-05-12	0	4	Young	Young				Incubation	
2000-05-13				Young				Young	
2000-05-14				Young				Young	
2000-05-15				Young	0	6	Young	Young	
2000-05-16				Young				Young	
2000-05-17				Young				Young	
2000-05-18				Young				Young	
2000-05-19				Young				Young	
2000-05-20				Young				Young	
2000-05-21								Young	
2000-05-22								Young	
2000-05-23								Young	
2000-05-24								Young	

Nesting parameters: estimated clutch size = 4 eggs; minimum clutch size = 3 eggs; maximum clutch size = 6 eggs; laying interval = 1 day; onset of incubation = with the last egg laid; length of incubation = 10 days; and length of rearing period = 12 days.

Example 3: Nest record reporting occurrences of four eggs and four young. The chronology was positioned according to the algorithm used when only incubation and rearing observations are available.

Example 4: Nest record reporting occurrences of five eggs and six young. Because the number of young is larger than the number of eggs observed earlier, laying was implied after the 5th egg and the algorithms from the *rNest* package completed the clutch size to the maximum number of young seen. Because incubation starts with the last egg laid, the laying stage lasted 5 days.

Figure 1.6. Examples of fictitious nest records from the package *rNest* with two observations (visits).

Example 5

Date	Observation		Backcalculation	
	Egg	Young	Nesting stage code	Nest chronology
2000-04-26				Laying
2000-04-27				Laying
2000-04-28				Laying
2000-04-29				Incubation
2000-04-30				Incubation
2000-05-01				Incubation
2000-05-02	4	0	Incubation	Incubation
2000-05-03				Incubation
2000-05-04				Incubation
2000-05-05				Incubation
2000-05-06				Incubation
2000-05-07				Incubation
2000-05-08	4	0	Incubation	Incubation
2000-05-09	1	3	Hatch	Young
2000-05-10				Young
2000-05-11				Young
2000-05-12				Young
2000-05-13				Young
2000-05-14				Young
2000-05-15				Young
2000-05-16				Young
2000-05-17	0	4		Young
2000-05-18				Young
2000-05-19				Young
2000-05-20				Young
2000-05-21				
2000-05-22				
2000-05-23				
2000-05-24				

Example 6

Date	Observation		Backcalculation	
	Egg	Young	Nesting stage code	Nest chronology
2000-04-26				Laying
2000-04-27				Laying
2000-04-28				Laying
2000-04-29				Incubation
2000-04-30				Incubation
2000-05-01				Incubation
2000-05-02				Incubation
2000-05-03				Incubation
2000-05-04				Incubation
2000-05-05				Incubation
2000-05-06				Incubation
2000-05-07				Incubation
2000-05-08				Incubation
2000-05-09	0	4	Young	Young
2000-05-10	0	4	Young	Young
2000-05-11				Young
2000-05-12				Young
2000-05-13				Young
2000-05-14				Young
2000-05-15				Young
2000-05-16				Young
2000-05-17				Young
2000-05-18				Young
2000-05-19				Young
2000-05-20				Young
2000-05-21				Young
2000-05-22	0	4	Young	Young
2000-05-23				
2000-05-24				

Nesting parameters: estimated clutch size = 4 eggs; minimum clutch size = 3 eggs; maximum clutch size = 6 eggs; laying interval = 1 day; onset of incubation = with the last egg laid; length of incubation = 10 days; and length of rearing period = 12 days.

Example 5: Nest record with a number of eggs and young indicative of a hatching date. All nesting stages were estimated according to the hatching date.

Example 6: Nest record with three widely spaced observations (visits) of four young. Observations imply that the rearing stage lasted longer than the theoretical period. In this case, the algorithm did not extend the rearing period beyond the observations.

Figure 1.7. Examples of fictitious nest records from the package *rNest* with more than two observations (visits).

1.7 Results and Discussion

The backcalculation algorithms developed were applied to 85% of all the records reported in the NestWatch database (BSC, 2013), which represented 202,407 nest records and 478,419 nest visits. The remaining 15% were discarded because they were incompatible with the algorithms (e.g., observations of nest building or of fledged young). Half of the nests were only visited once, and only 19% were visited more than three times. In the case of multiple visits on the same day, only one of the visits was used, and this typically corresponded to the latest nesting stage observed for that date, except if one of the visits had information about laying, hatching and/or nest departure.

All nest visits used were given a nesting stage code (Table 1.2) based on the number of eggs and/or young, and on the nesting stage code of the previous visit. In the majority of cases, this was either “incubation” (32%) or “young” (31%). Only a small proportion of observations were given the nesting stage codes “laying” (8%), “hatch” (2%) or “fledging” (2%), which are associated with a minimum level of uncertainty concerning the nest initiation date. Species with the highest proportion of the latter three nesting stage codes were ground nesters, including most waterfowl. At the other end of the scale, 21% of visits received nesting stage codes “unknown” (12%), “nest” (5%) and “active” (4%), which are associated with a maximum level of uncertainty concerning the nest initiation date. Species with the highest proportion of these nesting codes were those for which the content of the nest is difficult to assess, such as cavity or canopy nesters, or those building hanging nests. For example, 58% of Bullock’s Oriole nests (hanging nests), 53% of Red-naped Sapsucker nests and 46% of Bushtit nests (cavity nesters) fell into one or other of these code categories. Finally, a few visits received the nesting stage code “eggs” (4%) when there was no clear distinction between the laying and incubation stages.

The mean backcalculation index of uncertainty varied from 1 day (low) to 65 days (high); however, 95% of the species had a mean index value equal to, or lower than, 25 days.

The highest mean backcalculation uncertainty was associated with species with long nest chronologies. These tended to be large species with difficult-to-access nests, such as raptors (e.g., Bald Eagle (uncertainty value of 65 days), Golden Eagle (61 days) and Gyrfalcon (48 days)) and herons (e.g., Great Egret (41 days) and Great Blue Heron (37 days)).

A summary of the classification of observations for each species, the relative proportion of

nesting stage codes, the proportion of nests with minimum uncertainty, and the mean backcalculation uncertainty are provided in Panel 3 of Part 2 – *Species Accounts*. As mentioned earlier, this panel also provides the values of the theoretical nesting parameters used in the backcalculation procedure.



(Photo: Nest, egg and young of Double-crested Cormorant; B. Drolet)

CHAPTER 2: MODELLING NESTING PHENOLOGY

2.1 Introduction

While Chapter 1 covers the succession of nesting events at the nest scale, this chapter focuses on predicting when the nesting of a given species, or group of species, occurs at the scale of the Canadian breeding range. However, two major challenges arise when using nest records from citizen science programs, such as Project NestWatch (BSC, 2013) or breeding bird atlases, to make such predictions. Firstly, for most regions of Canada, and this is especially so for the north, there are too few nesting observations available to allow an accurate description of the nesting season to be derived solely from local observations. In fact, most observations are concentrated in or around the inhabited regions of Canada, of which the majority are located in the southern part of the country. A method was thus required to provide a meaningful portrait of the nesting phenology across the different regions of Canada that accounted for this lack of data in its estimations. Secondly, the number of nest records varies considerably among species and regions, and so if all nest records are used, and no attention is paid to the local relative abundance of nest records for different species, the constructed nesting calendars are unlikely to be representative. For example, in most inhabited regions there are relatively few nest records reported for certain species, but a lot of records for more familiar species, such as the American Robin or Tree Swallow (see Chapter 1). One way to account for the varying amount of information across regions and species is to model the nesting phenology of each species within its breeding range, and so derive species and region specific predictions. This allows predictions to be made in regions with little data, and also allows the production of general nesting calendars weighted with species-level predictions.

It is well known that the nesting period in birds is ultimately determined by the availability and abundance of an adequate food supply (Daan *et al.*, 1989), which, in turn, is partly influenced by environmental and climatic conditions (Dunn, 2004). The onset of nesting is thought to be positioned so that the abundance of food peaks when young need to be fed. In the case of insectivorous birds, nesting occurs when insects are more abundant, which generally coincides with the warmest months of the year. At higher latitudes, the period during which temperatures are warm enough to ensure a high abundance of insects is shorter, which reduces the window during which birds can breed. Thus, nesting is generally later and more synchronous in higher

latitude and colder regions (Carey, 2009).

Several environmental variables may be related to the availability of food resources and the onset of nesting in birds. Since environmental and climatic data are more readily available than data on food resources, the possibility of modelling the nesting phenology of birds using relevant environmental variables was explored.

2.2 Modelling information

Environmental data

The National Ecological Framework for Canada (Marshall *et al.*, 1999) contains an ecological land classification according to various geological, ecological and climatic factors. Within this framework, land in Canada is subdivided according to a hierarchical scheme, the result of which is a set of 1,021 ecodistricts characterized by several climatic and ecological characteristics (Figure 2.1). The measurements provided for each ecodistrict include the minimum, maximum and mean monthly and annual temperatures, and precipitation levels; the growing degree days; and the growing season. All of these figures are highly correlated with one another, making it difficult to use more than one variable to describe the timing of the nesting season. Moreover, certain measurements are not available for, or applicable to, all ecodistricts (e.g., number of growing degree days > 5 in the Northern Arctic). One variable that is obviously likely to have an important influence on the onset of nesting is the mean annual temperature (MAT), which varies substantially across Canada. Furthermore, unlike the other categories, temperature variables were available for almost all ecodistricts (Figure 2.2).

Initially, it might appear reasonable to assume that nesting phenology in birds should be more strongly linked to temperatures experienced during or prior to the nesting season. This assumption was tested using the MAT and each mean monthly temperature as explanatory variables in the final models, and these were compared using the Akaike Information Criterion (AIC) (Burnham and Anderson, 2002). Details concerning this analysis, and the reason why MAT was finally chosen instead of other measures of temperature, are fully described in the following section.



Figure 2.1. Ecodistrict divisions in Canada (thin gray lines; $n = 1,021$) according to the National Ecological Framework for Canada (Marshall *et al.*, 1999). Each ecodistrict is characterized by several ecological and climatic factors, including the mean annual temperature.

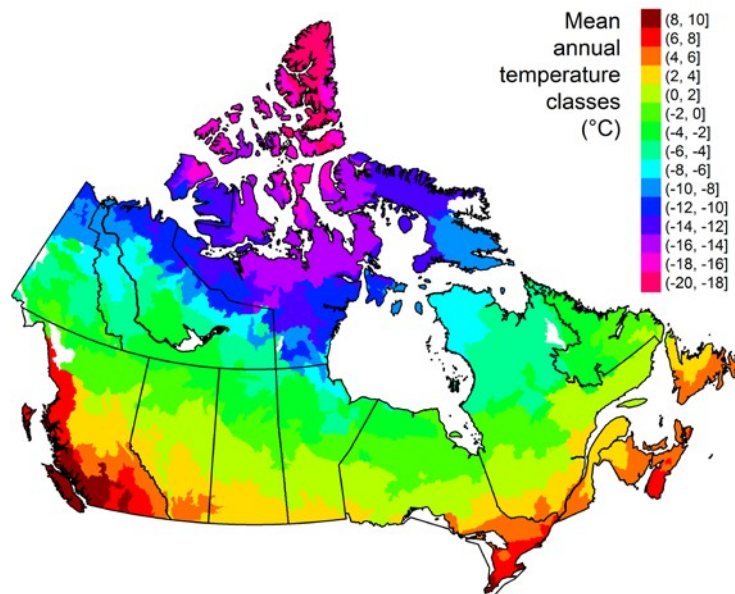


Figure 2.2. Mean annual temperature of the 1,021 ecodistricts in Canada according to the National Ecological Framework for Canada (Marshall *et al.*, 1999). Land areas in white are ecodistricts without mean annual temperature data.

Nest records

The models were built using a selection of nest records ($n = 200,528$), mainly from the Project NestWatch database (198,322 nest records for 335 species; BSC, 2013). How nest records were selected from the database is described in Section 2.3. The dataset used for the present study was completed using selected nest records from the Northwest Territories (1,478 nest records for 127 species; EC, 2014) and Nunavut (728 nest records for 46 species; Coulton and Robertson, 2009). The nest chronologies were estimated using the backcalculation procedure described in Chapter 1.

The ecodistrict dataset was used to attribute temperature data to every georeferenced nest contained in the final database. Nest records from the few ecodistricts lacking temperature data were excluded from the analysis. In certain cases, the coordinates associated with a given nest record were not precise. When it was possible to determine in which ecodistrict such nest records were recorded, the coordinates of the centroid for that ecodistrict were used as a surrogate location, so allowing a MAT value to be associated with the record. For most nest records in British Columbia, nest locations were derived using the centroid of the survey square from the breeding bird atlas grid in which the nests had been observed.

Breeding distribution

Range maps for species breeding in Canada were originally obtained through NatureServe (2013) as Environmental Systems Research Institute, Inc. (ESRI) Shapefiles. These data are now merged and available through the database provided by BirdLife International (Ridgely *et al.*, 2003). The potential presence of a given species within an ecodistrict was determined by intersecting the breeding distribution map for the species with the ecodistrict map. The list of bird species regularly breeding in Canada was compiled by Marie-Anne Hudson (EC, 2015b). Panel 3 of Part 2 – *Species Accounts* provides a map of the ecodistricts in which a given species is reported to nest.

2.3 Modelling procedure

Environmental variables and biological characteristics can help determine when species are likely to nest in a given region. However, the variability among individuals and the inter-annual variations in climatic conditions also influence the laying date of the first egg in a given

population, and between nesting seasons. One way to describe this variability, and to provide an idea of the intensity of nesting at a given point in time, would be to describe the nesting season of a species in a region using the proportion of active nests at any given moment in relation to potential explanatory variables (Figure 2.3). This could be achieved using Generalized Additive Models (GAMs) that can describe functional relations of unknown shape, as would be the case for the proportion of active nests throughout the nesting season. However, to produce reliable estimates of nesting activity, this approach would require a sufficient sample size for every location of interest, or for each combination of explanatory variables. Furthermore, GAMs are not well suited to predicting responses outside the range of observations, which is required for estimating the phenology of nesting across Canada. For these reasons, a simpler approach was chosen, under which it was possible to circumscribe the period when the bulk of the nesting occurs, instead of trying to estimate the precise pattern of nesting phenology within the season for each species. This approach allowed the construction of a predictive model for each species across its breeding range, despite the occasional presence of regions with sparse or inexistent data.

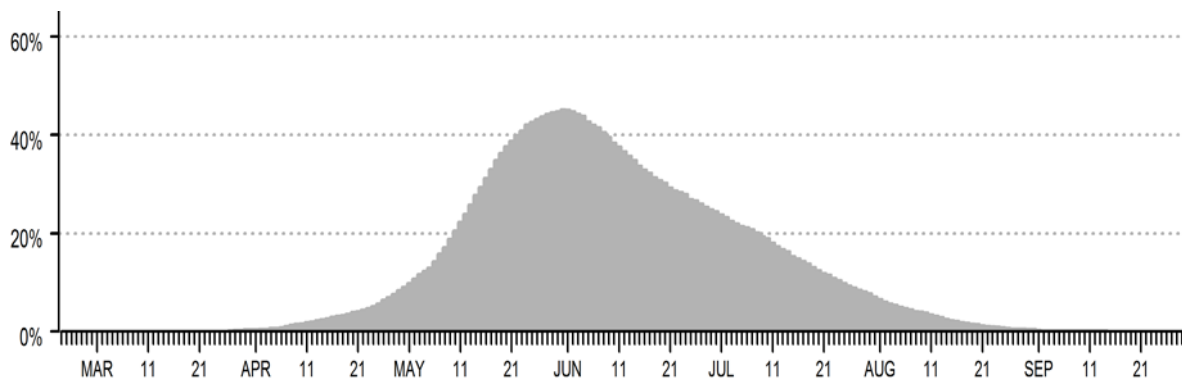


Figure 2.3. Proportion of active Song Sparrow nests across the nesting season, based on the 4,588 nest records retained for the analyses. The nesting season begins in April, has a peak in activity around the first week of June, and ends in August.

Quantile regression

The quantile regression was used to describe the beginning, midpoint and end of the nesting period for every species. Instead of estimating the mean response, quantile regression allows the estimation of the response at selected quantiles (Figure 2.4; Cade and Noon, 2003). For example,

instead of estimating the mean date at which the first egg is laid, it is possible to estimate the date at which a certain percentage of nests had a first egg laid. This allowed the nesting season of a species to be circumscribed by estimating the date by which most first eggs will have been laid and when most nests will have been vacated by young.

Firstly, two models were built using the first egg date and the nest departure date in Julian days for each nest record as response variables. The dates used were the backcalculated ones from the *rNest* package (See Chapter 1). To reduce the impact of unusual nest records that were particularly early or late, and to eliminate possibly aberrant observations or keyboard data errors, we chose to estimate the 10% quantile for the first egg date and the 90% quantile for the nest departure date. Although these percentages might appear to exclude a large proportion of nests, the quality of the nest observations in the database is highly variable, due in part to the absence of data validation. Using a more inclusive period (e.g., 1% or 5%) would have given too much importance to extreme or aberrant observations. Moreover, the uncertainty in the estimation of nest chronologies associated with backcalculations can artificially extend the period when nests are found, especially when a nest was observed at the beginning or at the end of the nesting period, and this effect is even more important when there is only data for a single nest visit (see Chapter 3 for a discussion on uncertainty and bias).

To obtain an idea of the variation in the peak nesting activity across regions, a third model was built to estimate the date at which 50% of nests will have reached the midpoint of their active period. To do so, the middle date of each nest chronology was calculated and used as a response variable. By definition, peak nesting activity is the moment at which most nests are active, but this would have required a different modelling approach. Instead, to represent the nesting season midpoint, it was decided to remain within the quantile regression framework and to provide an estimate of when the nesting period was halfway through.

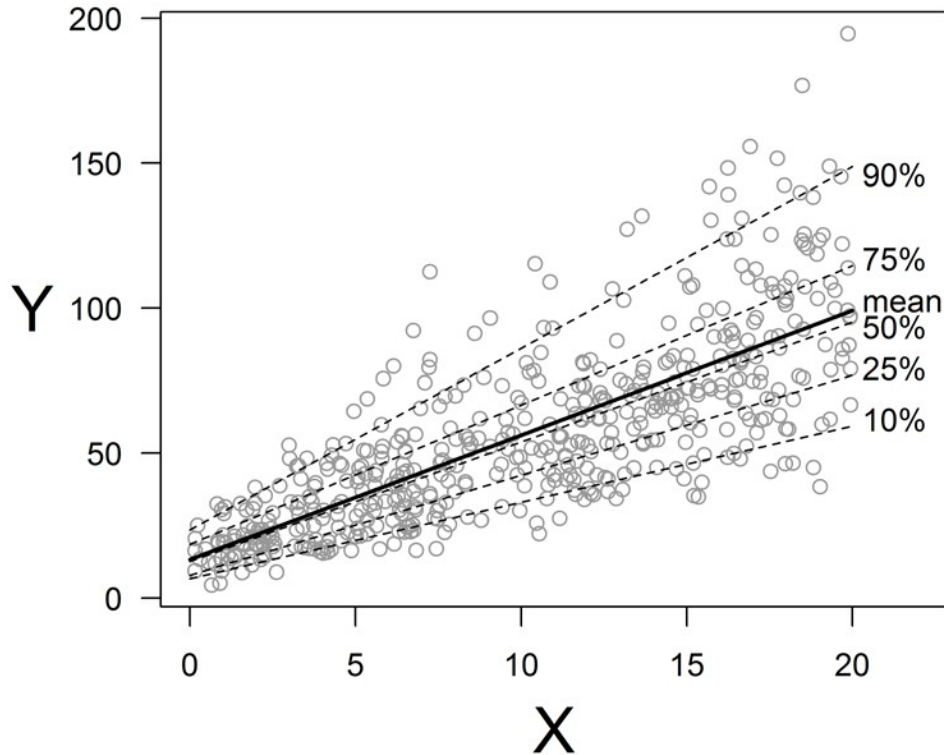


Figure 2.4. Examples of quantile regression with predictions at selected quantiles. The 10%, 25%, 50%, 75% and 90% quantiles are estimated. The mean response estimated using a classical linear model is shown for comparison.

Shape of the relation between temperature and nesting phenology

Initial data exploration suggested a non-linear relationship between temperature and both the first egg and nest departure dates. Therefore, a transformation was sought that would provide an acceptable fit between temperature and the selected response variables. Biologically speaking, two assumptions can be made concerning the relation between temperature and the laying of the first egg. Firstly, it is reasonable to assume that first egg dates should not be earlier under harsher climatic conditions (e.g., with a lower MAT), and secondly, the length of the nesting season is likely to be at least equal if not shorter under harsher climatic conditions, than under milder climatic conditions.

This imposes constraints on the shape of the first egg curve, and on the shape of both the first egg and nest departure curves relative to one another. The first assumption requires that the prediction curve for the date by which 10% of first eggs were laid should not increase with increasing in MAT. The second assumption implies that the prediction curves for the first egg

and nest departure dates should be parallel or form a cone-shaped pattern, indicating a shorter length of the nesting season with decreasing temperature. As long as both curves respected the second criterion, there was no restriction placed on the shape of the nest departure curve. There was also no prior expectation concerning the timing of the end of the nesting season in relation to climatic conditions. It could conceivably end earlier in the south for species with a well circumscribed nesting season, while it could end later for species with a more prolonged nesting season, or for species producing multiple clutches.

Although many functional forms respond to these criteria, two of the more commonly used ones, the logarithm and the square-root transformation, were explored to produce data transformations that were compatible with the chosen assumptions. The decreasing pattern of the first egg curve with an increase of MAT values can be obtained using both. The square-root transformation was preferred to the log transformation as, in many cases, the latter led to a sharp advance in the timing of nesting in warmer regions and an unrealistically early first egg date in colder regions. The square-root transformation was felt to lead to more realistic predictions and to a better visual fit with the data. Because the temperatures used were in Celsius, the local temperature was subtracted from the maximal temperature encountered to avoid negative values during transformation.

Determining which temperature to use

To determine whether different measures of temperatures were superior to the MAT for predicting nesting phenology, 13 candidate models were built using MAT and the 12 mean monthly temperatures for the first egg, the midpoint and the nest departure models, and these were ranked according to their AIC values. For the set of models for first egg date and the midpoint, those using MAT were superior (Table 2.1). In fact, temperatures experienced during the nesting season proved to be the least reliable for predicting the beginning of the nesting season. One possible explanation for this may be that the MAT better integrates important aspects related to bioclimatic conditions that affect bird nesting phenology. For the nest departure model, however, the best one was that which used the mean temperature for June, with the MAT model ranking sixth. The explanation for this is unclear, as there was a range of different months that ranked as the first model for the beginning, the middle and the end of the nesting season. The MAT was chosen for all three dates because the first egg date was the date

that showed the most variation across regions, and the MAT provided the best fit for estimating this. Moreover, using a single measure of temperature simplified the interpretation of the models and the presentation of the results.

Table 2.1. Difference in Akaike information criterion (Delta AIC) values between models using the different mean monthly temperatures and the mean annual temperature (MAT, in bold) for the first egg, midpoint and nest departure models

First egg	Delta AIC	Midpoint	Delta AIC	Nest departure	Delta AIC
MAT	0	MAT	0	JUN	0
DEC	2,961	OCT	275	SEP	166
NOV	3,891	SEP	349	JUL	397
JAN	4,183	NOV	1,313	MAY	499
APR	4,309	MAY	1,589	OCT	681
OCT	4,466	DEC	1,892	MAT	950
MAR	5,855	APR	2,481	AUG	1,045
FEB	6,705	JAN	2,750	APR	1,213
SEP	9,785	JUN	2,937	NOV	1,305
MAY	11,838	MAR	3,320	DEC	1,721
AUG	20,263	AUG	3,588	MAR	1,784
JUN	21,847	FEB	3,722	JAN	1,950
JUL	24,090	JUL	3,892	FEB	2,011

Model formulation

The MAT was the main predictor variable to which the timing of nesting was linked. However, the relationship between the MAT and the timing of nesting may differ among species due to their different biological characteristics. For example, resident species might start breeding earlier in southern or more temperate regions, while nesting in the north might be greatly delayed due to harsher climatic conditions (e.g., important snow cover). By contrast, when compared to species arriving earlier, neotropical migrants arriving late on their breeding grounds might start to breed as soon as they arrive, with the timing of nesting being more or less the same across southern and northern regions. Ideally, the precise relationship between the MAT and nesting phenology should be determined for every species, as each may have different biological characteristics. However, this would require a huge amount of observations covering the

different temperatures experienced by the species across its breeding range. This was not the case for most species within the database considered, and although the relationship between nesting phenology and MAT was determined for every species using species-specific models, this led to nonsensical results for many species. Nevertheless, imposing the same relationship between MAT and nesting phenology to every species also led to a poor fit for some species. Therefore, a compromise was sought that would allow a reasonable fit for most species by controlling the flexibility of the relationship using general grouping variables (Table 2.2). Thus, all other variables in the models, except the species itself, were included to adjust the relation between MAT and the nesting phenology of different groups of birds. Specifically, along with the species considered as a factor in the models, two-way interactions were included between the MAT and the following three variables: the migratory strategy (i.e., resident, short, mid- or long distance migrant); the tendency to breed early or late; and the capacity to lay multiple clutches (i.e., single or multiple; Table 2.2). This also allowed the slope of the relationship to be dependent on the latter three variables (see Panel 4 of Part 2 – *Species Accounts* for the values of the variables used for each species).

Table 2.2. Model structure and composition used to predict the nesting phenology of birds in Canada. First egg, nesting midpoint and nest departure Julian dates were used as response variables for the beginning, middle and end of the nesting period. Explanatory variables are the mean annual temperature (MAT), the migratory strategy (mig), the tendency to breed early or late (breeder), the capacity to lay multiple clutches (mclutch), and the species. The “:” symbol denotes interactions with the MAT

Predicted value	Model
First egg date	MAT + MAT:mig + MAT:mclutch + MAT:breeder + species
Nesting midpoint date	MAT + MAT:mig + MAT:breeder + species
Nest departure date	MAT + MAT:mig + MAT:mclutch + species

Although one species may have more than one migratory distance strategies across Canada, a single migratory distance strategy was attributed to every species. This was done to reduce complexity and because of the lack of sufficient data to precisely categorize the migratory strategy of all species across their breeding range. The classification of migratory strategies was done using recently published range maps (Sibley, 2012) and the following four criteria: species were considered “resident” if there was no true migration; “short distance migrants” if migration

was limited to the northern part of the U.S.A.; “mid-distance migrants” if migration was limited to the southern part of the U.S.A.; and “long distance migrants” if migration extended beyond the southern part of the U.S.A.

Initially, only migratory strategies were used in interactions with MAT. However, in many cases, this led to a poor fit, because of species with similar migratory distances having very different life histories (e.g., the Osprey and Blackpoll Warbler are both “long distance migrants”). Along with migratory strategy, species were further categorized as “early” or “late” breeders (tendency) based on the timing of nesting using backcalculated first egg dates. Specifically, species were categorized as “early” breeders if 2% or more of all first eggs were laid on or before April 20th; if not, they were categorized as “late” breeders. The choice of 2% and April 20th was subjective, but they performed better than others in improving the fit of the models. Some species that did not have enough observations to pass the 2% threshold were nonetheless categorized as “early” breeders, as this improved the fit of their models. The tendency to breed early or late was only used in the models for the first egg date and nesting midpoint, as the timing of nest departure seemed less variable within species. Finally, a binary variable, “single” or “multiple”, was included to account for whether a species lays a single clutch within a given nesting season or has the capacity to lay multiple clutches. Species that only regularly lay multiple clutches in the south, or in certain parts of Canada, were usually considered as multiple clutches.

Understandably, species typically laying multiple clutches often have longer nesting seasons in the south than species laying single clutches.

In summary, the slope of the relation between the MAT and nesting phenology was determined by the migratory strategy, the tendency to breed early or late, and the capacity to lay multiple clutches; while the intercept (or height) of prediction curves was determined by species (Figure 2.5). One major advantage of grouping species using characteristics based on their biology was that, for a given species, this grouping provided extra data from all similar species. This facilitated the extrapolation of predictions outside the range of the MAT for which nest observations were available, as all species under the same grouping variables were considered to have the same relation between the MAT and nesting phenology. In other words, by assuming that the nesting phenology of species with similar characteristics had a similar response to MAT, it was possible to estimate the nesting phenology of species for which there were few

observations. This was done using predictions that were ultimately determined by all species with the same characteristics. The set of variables and the model formulation used thus represented a compromise between providing flexibility to the models to allow better species- level predictions, and maintaining the ability to make predictions for species with too few observations to provide reliable predictions based solely on their data. It should be noted that the grouping variable “capacity to lay multiple clutches” was eliminated from the nesting midpoint model, because the model containing all variables was not valid, and eliminating other variables led to more serious problems fitting prediction curves to observations.

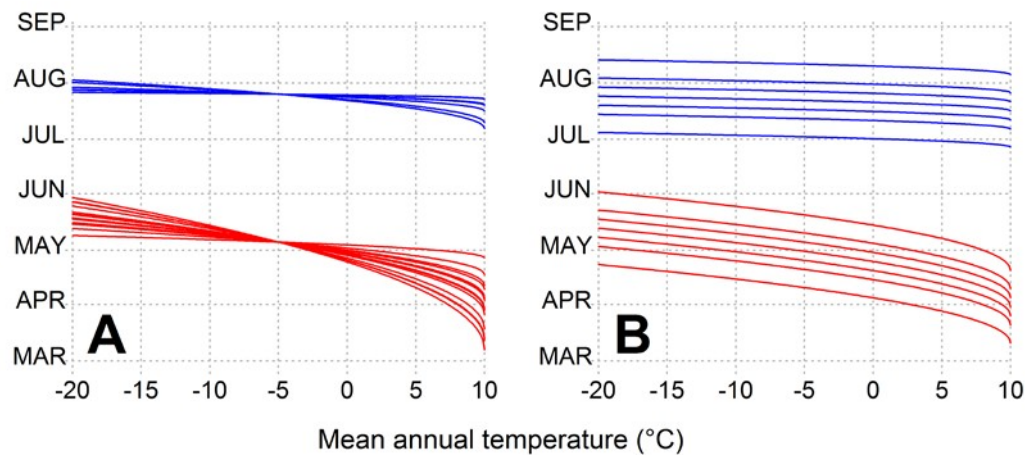


Figure 2.5. Consequence of model formulation on the shape and position of prediction curves. A) Illustration of the different possible slopes according to the interactions between mean annual temperature and each of the grouping variables: migratory strategy, tendency to breed early or late, and whether a species lays multiple clutches within a single nesting season. B) The intercepts (heights) are determined by species.

Weights

To account for the varying quality and quantity of nest observations among nest records when estimating model parameters, observations were weighted to give more influence to those nest chronologies estimated with higher certainty (see Chapter 1, Section 1.5 for details). Weights were also used to give each species the same level of influence on the determination of the slope of the prediction curves.

Different measures can be used to adjust the relative influence of nest records according to their

uncertainty. One option is to use a weighting factor equivalent to the value of 1 divided by the uncertainty associated with each nest record. For example, a nest record with an uncertainty of 1 day would get a weight of 1, and a nest with an uncertainty of 2 days would get a weight of 0.5. This weighting is thus based on the *multiplicative inverse of the backcalculation uncertainty*. However, this approach gives a great deal of influence to certain nests, which may reduce the effective sample size and lead to unexpected results when few nests are available for a given species. To reduce the influence given to specific nests using this method, an alternative weighting factor based on *the percentage of uncertainty compared to the length of the active period* was used. Specifically, for each nest record, the uncertainty in number of days was subtracted from the theoretical nesting period, and the ratio between the result of this subtraction and the theoretical duration was calculated. Furthermore, 1 was added to the numerator to avoid values of 0. For example, a nest record for which the uncertainty was estimated to be 10 days with an active period theoretically lasting 30 days was given a weight of 0.7 (i.e., $(30 - 10 + 1) / 30$). Thus, the weighting obtained was a value comprised between 0 and 1, where values closer to 1 had a greater influence on the model or when estimating the parameters of the models. Although some nest records were assumed to be backcalculated without uncertainty, it is important to keep in mind that this weight value was not intended to estimate the level of confidence in the specific backcalculated dates. Rather, it gives a greater influence in the modelling process to nest records with higher quality observations and for which the estimated certainty is higher (see Chapter 3 for a more thorough evaluation of why this weighting method was used).

A second weighting factor was used to give the same influence to each species in the estimation of the slope of the relationship between the MAT and both the first egg and nest departure dates. As species with more nest records would have had more influence on the estimation of the slope of the prediction curves, this allowed an equal influence across species without affecting the estimation of the intercept associated with each species. Each nest records received a weight equals to 1 divided by the number of nests for that particular species, such that the sum of all weights for a given species equaled 1. This second weighting was then multiplied with the first weighting described above to obtain a final weighting that was used in the models for each nest record. Thus, the final weighting took into account the higher quality observations and it also standardized the influence of different species on the estimation of the slope of the models.

Nest records and species rejected

To reduce the impact of possibly aberrant observations or backcalculated chronologies, or of erroneous data entries on the modelling process, nest records for which the length of the inferred nesting period differed by more than 30% from the theoretical nesting period (either longer or shorter) were discarded from the analysis. Rejected nests accounted for less than 1% ($n = 1,879$) of all nest records considered for the backcalculation (Chapter 1, see Section 1.7). In many cases, rejected nest records seemed indicative of second clutches within the same nest, or incomplete, aberrant or wrongly transcribed nesting observations that were not easily interpretable by the *rNest* package.

In the case of precocial species, and also Gray and Steller's jays, many observations in the Project Nestwatch database concerned the observation of young. In many cases, these observations seemed to be only of young that had already left the nest and that should not have been coded as "young" (e.g., the observation of a brood of ducklings). For these species, initial analyses produced nest departure dates that appeared to be unacceptably late, which suggested that the influence of young observed out of the nest was non-negligible. Therefore, unless a status code was used to indicate that young were still in the nest or had just left, it was decided to eliminate all nest records of precocial species (and the two jays) for which there were only observations of young. Originally, Project NestWatch was not designed to account for such observations, and consequently, there was no specific algorithm developed in the *rNest* package to backcalculate nest departure dates using young observed out of the nest. However, new status codes have been added, which in the future will allow for better coding of observations of young out-of-the-nest and facilitate backcalculation of the nesting chronology of species with precocial chicks.

The range maps of species were also used to eliminate clearly mislocated nest records from the modelling process. However, for certain species, where multiple observations were reported outside the established breeding range, these were retained when they were either very close to the accepted breeding range, according to the range maps provided by BirdLife International (Ridgely *et al.*, 2003), or when they fell within the limits of other digitally published range maps (Dunn and Alderfer 2011, Sibley 2013). The map provided in Panel 3 of Part 2 – *Species Accounts* show the breeding range used and the locations of the nest records for each species

considered. Finally, species with 10 nest records or less remaining after the backcalculation process were discarded.

Model estimation and selection

As the nesting phenology models were designed to provide predictions beyond the range of observations for several species, one challenge with the analysis was to ensure that predictions made biological sense in regions for which data were lacking. In such situations, there are no statistical measures that could help determine whether predictions were accurate or biologically meaningful. For this reason, the set of variables and the model structure chosen were those felt to best represent the available data concerning the breeding birds of Canada, and that led to the best predictions according to current general knowledge and that of regional experts. The aim was not to make inferences concerning the effect of variables included in the models, but rather to obtain an acceptable fit between prediction curves and observations, as well as a satisfactory prediction for regions outside the range of observations (see Chapter 3 for a more detailed discussion on uncertainties and potential biases). The fit of all models was scrutinized visually and unsatisfactory ones were discarded.

All analyses were run using R 3.1.1 (R Development Core Team, 2010), using the quantreg 5.05 package (Koenker, 2013) and the Frisch-Newton interior point method, to allow for faster parameter estimation. Confidence intervals around prediction curves were obtained by bootstrapping using the quantile method with subsets of 20,000 observations containing 10% of the initial dataset and 50 replicates.

2.4 Results and Discussion

Overall, 200,528 nest records were processed and nesting predictions were provided for 311 species, which represents 71% of the 439 species known to nest in Canada (EC, 2015b). The lack of a prediction for a given species was mainly due to an insufficient number of nest records (63 with no nest records and 41 with insufficient data for modelling (generally 10 nest records or less)) or unsuccessful modelling (24 species). In the latter case, the models were rejected due to a poor fit with the available data (see below for more details). Model predictions were derived from the three models (i.e., first egg, midpoint and nest departure dates) and were restricted to the range of MATs experienced by a species within its normal breeding distribution. The nesting

phenology prediction for each species, and the confidence intervals and the values of the model parameters for all species are presented in Panel 4 of Part 2 – *Species Accounts*. Predictions for each species *and* for each ecodistrict are available on the Bird Studies Canada website under "Nesting Calendar Query Tool" in the NestWatch Program section (Rousseu and Drolet, 2015). This tool allows the user to create customized nesting calendars by selecting the species and regions of interest (Figure 2.6). Nesting calendars are constructed using the main portion of the nesting season. A given calendar can be sorted using up to ten categories of interest, namely species, ecodistrict, bird conservation region, ecoregion, nesting area, province and territory, federally protected status, habitat, nest type and species group.

Figure 2.7 shows an example of predictions for the Song Sparrow. The red dots are the backcalculated first egg dates for all 447 nests used for this species. The blue dots are the associated nest departure dates. The red line shows the estimated dates at which 10% of first eggs would have been laid in relation to the MAT. The green line shows the estimated nesting midpoint dates at which 50% of nests would have reached the middle of their active period. The blue line shows the estimated nest departure dates when 90% of young would have left the nest. Song Sparrows are predicted to start nesting at the beginning of May in warmer and more southerly parts of the breeding range, and at the beginning of June in colder and more northerly areas. Departure is predicted to be similar across regions with most young having left the nest by mid-July. In the case of this species, it has been grouped with other species considered to be short distance migrants, early breeders and multiple clutchers.

For most species, model predictions supported the two main assumptions, namely that the beginning of the nesting season should be earlier in warmer regions and that the length of the nesting season should be equal or progressively shorter with decreasing temperatures. Nest departure dates are usually later in colder regions, although species laying multiple clutches may end their nesting season slightly later in warmer regions than further north. This effect of temperature is also visible in most histograms showing the proportion of active nests per MAT class. The peak of curves associated with higher temperatures usually precedes the peak of the curves for nests found in colder regions (see Panels 2 of Part 2 – *Species Accounts*). In addition, the peak in the proportion of active nests associated with higher temperatures is also usually lower than that associated with lower temperatures, indicating that nesting is usually less

concentrated over time in warmer regions.

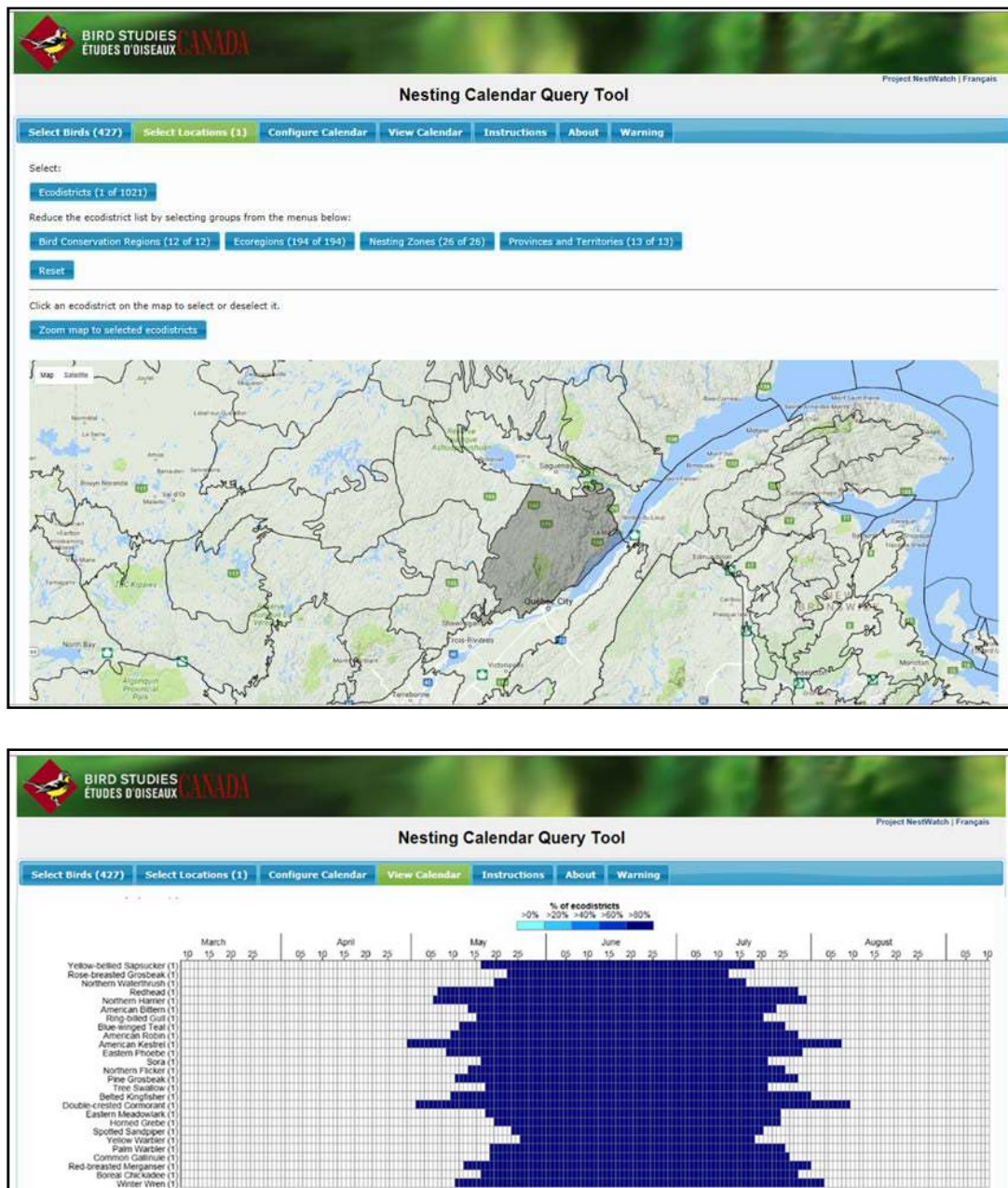


Figure 2.6. Screenshots of the Nesting Calendar Query Tool (Rousseu and Drolet, 2015). The upper one shows the Location Selection page. In this example, a single ecodistrict was selected (transparent gray screen) corresponding to the Lake Jacques-Cartier Highlands, north of Québec City. The lower one shows the nesting calendar with the predictions of the nesting periods of some of the species associated with the selected ecodistrict.

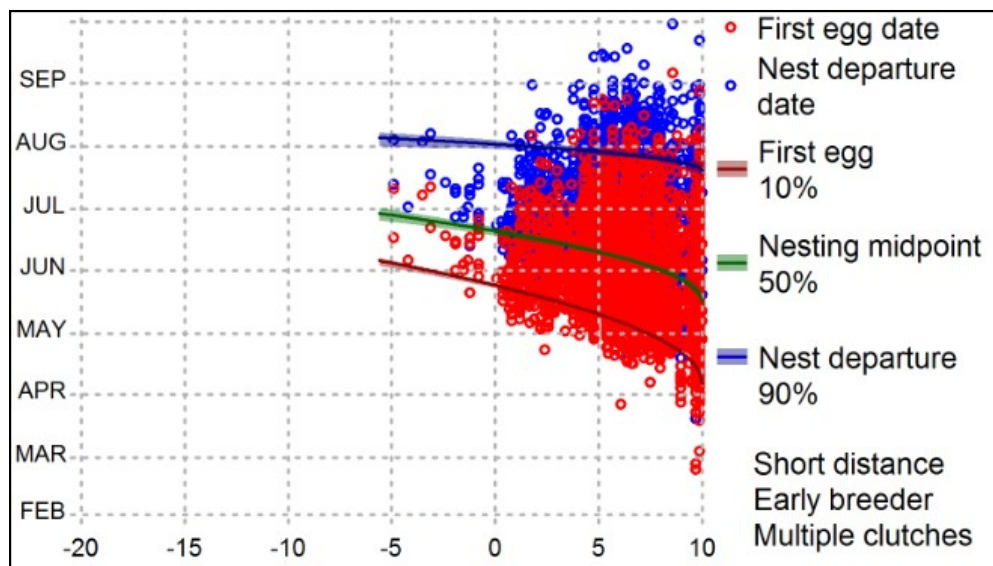


Figure 2.7. Example of predictions for the Song Sparrow ($n = 4,588$ nest records) derived from the models used to predict nesting phenology. The red dots are the backcalculated first egg dates and the blue dots are the associated nest departure dates in relation to mean annual temperature (MAT). The red line shows the estimated dates at which 10% of first eggs would have been laid; the green line shows the estimated nesting midpoint dates at which 50% of nests would have reached the middle of their active period; and the blue line shows the estimated nest departure dates when 90% of nests would have been vacated in relation to MAT (for other species, see Panel 4 of Part 2 — *Species Accounts*).

These two effects are especially pronounced in shorter distance migrants and species nesting earlier. These effects are much less pronounced in neotropical migrants, which are almost always classified as long distance migrants and late breeders, and in certain cases, the first egg and nest departure curves are almost parallel (see Panel 4 of Part 2 — *Species Accounts*), and first eggs are laid almost synchronously across the temperature range. The late arrival of these species on their breeding grounds, compared to earlier nesting species, probably contributes to the fact that the phenology of nesting is more similar across regions with different climates. Hence, for late- arriving long distance migrants, the beginning of nesting is almost the same for all regions, which leave less room for extended nesting periods. Thus, the effect of colder climates on the duration and the onset of the nesting season varies across species depending on their nesting strategy and their biology. Although these assumptions were made when selecting an appropriate

transformation of the MAT, a slope for the prediction curves was not specifically imposed to suit these assumptions and a given curve could have an increasing, flat or decreasing slope according to the data fitted.

Model fit

The aim was to attempt to model the nesting phenology of a large number of species within a single modelling framework. Considering the number of species for which predictions were to be produced, it was inevitable that some would be unsatisfactory. For most species ($n = 311$), the fit of the prediction curves was generally good. That is, in most cases, predictions for both the first egg and the nest departure dates appear biologically realistic across the temperature range of the breeding distribution of the species. (see Panel 4 of Part 2 – *Species Accounts* for a complete set of results). For 24 species, the fit was judged unsatisfactory as the nesting period appeared unrealistic and the predictions curves were discarded. The poor fit was mainly due to insufficient data to adequately cover the extent of possible MAT values within the breeding range (e.g., Surf Scoter, Black Guillemot and Great Black-backed Gull) and/or the length of the possible nesting season (e.g., White-winged Crossbill, Rock Pigeon and Barn Owl). Models were also discarded because of a lack of fit when predictions for first egg dates were too early (e.g., Osprey and Common Raven), or nest departure dates too late (e.g., Bald Eagle, Bohemian Waxwing and Swainson's Hawk). Finally, two species seemed to be separated into distinct populations that lacked similarity in the variation of the timing of nesting. For example, the Horned Lark is found in agricultural areas in the south, and above the tree line in the north. This produces a gap in the data with both populations seeming to have very different nesting periods. A similar situation is possibly responsible for the poor fit for the Canada Goose, which seems to be caused by the merging of two distinct nesting populations: the resident southern population and the migratory northern population. This particular case might also be influenced by the density of points in warmer zones, affecting the fit of the curve in colder ones.

Although many reasons may contribute to the lack of fit for a given species, few elements actually seem to be involved. One major factor was probably the compromise sought between allowing flexibility in the determination of the shape of the prediction curves for each species and the production of a realistic prediction for species with limited data. For the latter, it was impossible to obtain reliable prediction curves specific to the species because of the lack of data

or because data were only available for the southern part of the breeding range. The grouping of species imposes a shape to the prediction curve for all species within the group, but not all species within the group will necessarily have a similar nesting phenology. Therefore, this problem is mostly linked to the compromise between allowing flexibility in the determination of the curves and obtaining realistic predictions in colder regions for species with relatively few and concentrated nest records.

Establishing the shape of the relationship between nesting phenology and the MAT, or other environmental variables, can be difficult. The reasonable assumption that first egg dates should be later under harsher environmental conditions (e.g., colder temperatures or fewer growing degree days) imposes constraints on the shape of the curve predicting the first egg date. A square-root transformation was chosen in this study because it seemed to provide the best fit to the plotted data. However, a single transformation might not be appropriate for all species, or any group of species, because they could be responding differently to given environmental variables. In the absence of a wider geographical spread of data and without using a geographically-based approach, if more adaptive solutions like GAMs cannot be used, decisions need to be made concerning the actual shape of the relation.

In the case of nest departure dates, no clear assumptions can be made concerning the shape of the curve describing departure, or the link between the harshness of the climate and the timing of departure. Certain species or individuals nesting in milder regions could benefit by producing a second clutch or by delaying nesting until the end of the summer, thus potentially breeding later than in colder regions, where late breeding would be impossible. Other species could finish nesting earlier because they produce single clutches or because they are more synchronized within a season.

A related problem is how to account for the variability across species, because species in the models used only contributed to determining the intercept (or height) of the curves, not the slope (i.e., shape). Indeed, within a single grouping variable (e.g., migratory strategy), certain species may differ in the way they respond to variation in MAT. Thus the slope may not be suited for some species within the group. To assess the extent of this problem, individual species or groups of related species (e.g., warblers, sparrows or woodpeckers) were tested in interaction with the MAT (i.e., where each species or group of species was able to determine the shape of the curve),

but this led to too many species with aberrant predictions. This was probably due to low sample sizes and/or spatially or temporally correlated data. Therefore species level predictions were restricted by the use of grouping variables based on the migratory strategy, the tendency to breed early or late, and the capacity to lay multiple clutches. The use of these groups had the advantage of allowing the inclusion of species with fewer observations, and the predictions may also be more robust with regards to sampling artefacts and correlations within the data.

Despite similar MAT profiles, variations in other environmental parameters across regions could also be strong determinants for when birds nest. For example, two ecodistricts could have similar or identical MATs but different annual temperature ranges (e.g., coastal vs. continental climates), which may reduce the capacity to adequately predict the initiation and the end of the nesting period with a model strictly based on MAT. Some of the most problematic cases of this were associated with coastal and inland ecodistricts in British Columbia, such as the Fraser Lowland near Vancouver, where a milder year-round climate prevail, and the Okanagan Basin, which has colder winters and warmer summers, as these factors may influence nesting phenology. A method that can differentiate between these two types of climate should be employed. However, although efforts were made to take in to account this geographic effect (in the case of coastal areas in British Columbia and the Maritimes), this did not lead to an increase in the apparent likelihood of the predictions.

A major difficulty in this study was to represent the variation in climatic conditions across regions using a set of variables that were not too correlated, and that were available for all geographic locations. Since the objective was to predict rather than understand nesting phenology, the use of biologically relevant explanatory variables was not necessarily required if better predictor variables could be found. For example, had there been sufficient data for most/all species, and had the data available had a better geographical spread (rather than being concentrated around inhabited areas), another possible approach would have been to base predictions solely on geographical location. This would allow the integration of local environmental conditions that would influence the timing of nesting. One means of achieving this would be to use ecodistricts as variables, or as random effects, in a quantile regression mixed model. Predictions could then be made based on the ecodistrict, without any reference to environmental variables. This allowed possibly better predictions as it circumvented problems

associated with environmental variables that were not considered. For example, two ecodistricts with the same MAT would not be considered equal in terms of the timing of nesting, and instead they would be described by letting all their nest records determine the nesting phenology.

A second possible approach would have been to use additive models with geographic coordinates as variables or locally-weighted regressions, which would allow for predictions based on location. However, it can be difficult to obtain accurate predictions when trying to extrapolate outside the region in which the nesting data were gathered (Guisan *et al.*, 2002). In fact, none of these geographical approaches are possible for the moment, because of the current concentration of nest records in inhabited regions, and because of the lack of data for some species.

It is possible that there are correlational problems affecting some of the predictions presented, especially in the case of species with limited data. For example, if most nest records for a given species were collected in the same year and/or in the same area, the data available might not capture the year-to-year and/or the geographical variation in the nesting phenology of that species. One extreme example of this could be colonial species, where nesting can be highly synchronous. Currently, the Project NestWatch database does not differentiate between nests of colonial and non-colonial species, which means that multiple nests from a given colony, with almost identical information, will be treated separately. In certain cases, several nest records appeared to come from the same area, which suggests that observations were made at the same time with similar or identical nesting information being reported. This can cause problems because it inflates the numbers of nests used in the models, without providing the potential variation in nest chronologies across the breeding range of the species in question.

Finally, it should be noted that the dataset of temperatures for the different ecodistricts may not be appropriate for species found at high elevations. In most cases, the MAT values provided for a given ecodistrict represent the temperatures experienced in valleys, rather than in adjacent mountainous or alpine areas. Consequently, species nesting in alpine habitats are difficult to model, as the temperatures they experience at higher altitudes are likely colder than the MAT value reported for the ecodistrict. Unfortunately, the lack of precise locations for most nests from British Columbia, made it impossible to correct for elevation. For example, American Pipit nests in this province were associated with the MAT of the ecodistrict located at the centroid of the

atlas squares in which they were found, which may not correspond to the true MAT at the altitude where the species actually nests. This may partly explain the apparent inverse relationship with MAT for the American Pipit and the Gray-crowned Rosy-Finch (see Panel 4 of Part 2 - *Species Accounts*).

2.5 Future directions for improvements

In the future, certain aspects of the analyses used for the present study could be improved and other approaches could be explored to refine the quality of the nesting phenology predictions.

Target 1: Improve modelling. Using the existing data, the fit of the prediction curves could be improved in one of four ways: 1) finding another transformation or by using a different approach employing more flexible curves (e.g., GAMs, splines or locally-weighted regressions); 2) taking into greater account the variability across species, and the spatial and temporal correlations within the data; 3) using a geographically-based approach or a more relevant set of environmental variables to achieve better local predictions (see previous section for details); or 4) using Bayesian predictive models.

Target 2: Improve range maps. Further investigation into the timing of nesting would benefit from improved distribution maps. The range maps provided by BirdLife International (Ridgely *et al.*, 2003) were the only one available in ESRI (Environmental Systems Research Institute) Shapefile format that could be used to determine the presence of a given species in a given region of Canada. Although the quality of the maps appeared sufficient for most species, several were outdated or unsatisfactory (e.g., for Barrow's Goldeneye).

Target 3: Expansion of the Project NestWatch database. Further data, either contemporary or historical, are required to better portray the nesting phenology in certain areas (Figure 2.8), or for certain species (Table 2.3 and Part 2 – *Species Accounts*).

Gap 1: Northern Canada. There is a general lack of data for all species nesting in the northern part of Canada, especially in the northern Québec-Labrador peninsula and Newfoundland, in the northern part of the boreal forest across Canada, and in the Arctic (Figure 2.8).

Gap 2: British Columbia. When the Project NestWatch database was analysed (BSC, 2013), the only data from British Columbia was for landbirds. Although the results of this study suggest that some areas of the province appear well covered for non-landbird species, this is due to the fact that certain nesting zones shared with Alberta had data (Figure 2.8) for these species. Moreover, the location of the majority of the data available for British Columbia was imprecise because it was derived mainly from observations made during the breeding bird atlas, and the location use for each nest was the centroid of the 10km x 10km survey square that it was found in. Considering the altitudinal variation within this province, the lack of precision linked to nest locations could lead to less reliable predictions there than in other regions.

Gap 3: Waterbirds. Of the different bird groups, waterbirds had the largest data gap and this resulted in a lack of prediction for over 50% of species, compared to only about 25% in the other three groups (Table 2.3). This gap was expected as the citizen science-based Project NestWatch is mostly oriented toward landbirds and non-colonial species. However, historical nest records for waterbirds do exist. Therefore, future efforts to predict nesting phenology, could fill this gap by collecting and standardizing existing nest records from seabird and inland waterbird specialists in government agencies and universities. Nest records are especially needed for gulls, auks and other colonial seabird species.

Gap 4: Uncommon, local, rare or inconspicuous species. Waterbirds aside, gaps in the other bird groups were largely due to a lack of nest records for uncommon species or those with small breeding ranges (e.g., Dickcissel, Sky Lark and Common Poorwill); species at risk (e.g., Lewis's Woodpecker, Band-tailed Pigeon and Sage Thrasher); and species with nests that are generally hard to find (e.g., hummingbirds, swifts and owls), or that are located in habitats that are difficult to access, such as mountain tops, the boreal forest and the Arctic (e.g., White-tailed Ptarmigan, Northern Shrike, Black Scoter and many shorebirds; see Table 2.3).

Gap 5: New nesting species for Canada. There is a need to document the nesting phenology of species that have recently started breeding in Canada or that are spreading (e.g., California Quail, Chukar and Tufted Titmouse), and those that have been recently split in two and for which historical data cannot easily be allocated to the correct species

(e.g., the Pacific-slope and Cordilleran flycatchers, Cackling and Canada geese, and Winter and Pacific wrens).

Target 4: Establish the effect of altitude on nesting phenology. Where there is a significant variation in elevation within a given ecodistrict, it is reasonable to assume that nesting should be earlier in low altitude valleys, which are usually warmer than high altitude uplands where climatic conditions are generally harsher. Thus, in the case of a variation in altitude, the relationship between temperature and the date of laying should be similar to that of a variation in latitude. In mountainous ecodistricts, particularly those located in the Rocky Mountains, more accurate elevation data for nest record, along with well-defined changes in MAT with increased altitude, will be required for finer-scale predictions of nesting phenology.

Target 5: Monitoring the effect of climate change. This technical report provides a snapshot of the nesting phenology of birds in Canada according to observation made from the end of the 20th century to the beginning of the 21st century. As several aspects of bird phenology are known to be affected by environmental conditions, it is expected that nesting phenology will be influenced by climate change. An exploratory analysis of the data currently available from Project NestWatch (mainly from the mid-20th century to 2013; Figure 1.2) did not show a conclusive overall effect of climate change, but this is likely to alter as more contemporary data become available. In this context, it will be important to periodically reassess nesting phenology, so that potentially earlier nesting events may be taken into account. Interannual variations in climatic conditions might also be integrated into the analysis to take into account and better understand the effect of these variations on the nesting periods, and so, perhaps, enabling a better prediction of the nesting phenology for a given year, based on spring weather conditions.

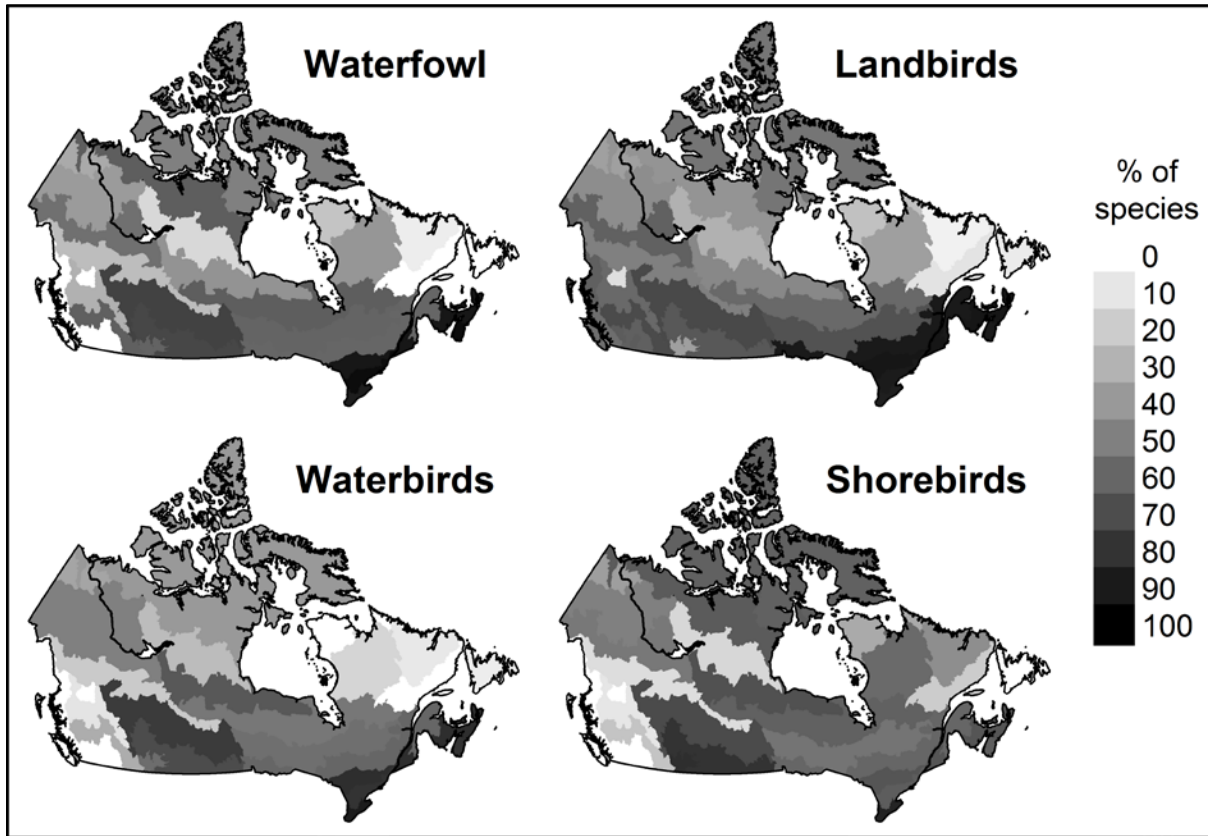


Figure 2.8. Percentage of species present in each nesting zone for which there was at least one nest record per bird group.

Table 2.3. List of nesting species in Canada not included in the predictions because of a lack of sufficient data (n = 104) or unsuccessful modelling (underlined, n = 24). Species with no nest record in the Project NestWatch database (BSC, 2013) are shown in bold (n = 63)

WATERBIRDS		
Yellow-billed Loon	Whooping Crane	Tufted Puffin
Western Grebe	Pomarine Jaeger	Black-legged Kittiwake
Clark's Grebe	<u>Parasitic Jaeger</u>	Ivory Gull
Northern Fulmar	Dovekie	Sabine's Gull
Manx Shearwater	Common Murre	Black-headed Gull
Fork-tailed Storm-Petrel	Thick-billed Murre	Ross's Gull
Leach's Storm-Petrel	Razorbill	Laughing Gull
Northern Gannet	Black Guillemot	Western Gull
Brandt's Cormorant	Pigeon Guillemot	<u>California Gull</u>
Great Cormorant	Marbled Murrelet	Thayer's Gull
Pelagic Cormorant	Ancient Murrelet	Iceland Gull
American White Pelican	Cassin's Auklet	Glaucous-winged Gull
Snowy Egret	Rhinoceros Auklet	<u>Great Black-backed Gull</u>
White-faced Ibis	Atlantic Puffin	Caspian Tern
Yellow Rail	Horned Puffin	Roseate Tern
LANDBIRDS		
California Quail	Northern Pygmy-Owl	Cassin's Vireo
Northern Bobwhite	Spotted Owl	<u>Gray Jay</u>
Chukar	Common Poorwill	<u>Common Raven</u>
<u>Ring-necked Pheasant</u>	Chuck-will's-widow	Sky Lark
Greater Sage-Grouse	Black Swift	<u>Horned Lark</u>
White-tailed Ptarmigan	Vaux's Swift	Gray-headed Chickadee
Dusky Grouse	White-throated Swift	Tufted Titmouse
Sooty Grouse	Black-chinned Hummingbird	Pacific Wren
<u>Sharp-tailed Grouse</u>	Anna's Hummingbird	<u>American Dipper</u>
<u>Osprey</u>	Rufous Hummingbird	Bluethroat
Mississippi Kite	Calliope Hummingbird	Northern Wheatear
<u>Bald Eagle</u>	Lewis's Woodpecker	Sage Thrasher
<u>Swainson's Hawk</u>	Williamson's Sapsucker	Eastern Yellow Wagtail
<u>Rock Pigeon</u>	Red-breasted Sapsucker	<u>Bohemian Waxwing</u>
Band-tailed Pigeon	White-headed Woodpecker	Kirtland's Warbler
Eurasian Collared-Dove	<u>Gyr Falcon</u>	<u>Harris's Sparrow</u>
<u>Barn Owl</u>	Pacific-slope Flycatcher	Dickcissel
Flammulated Owl	Cordilleran Flycatcher	<u>Gray-crowned Rosy-Finch</u>
Western Screech-Owl	Northern Shrike	<u>Red Crossbill</u>
<u>Great Horned Owl</u>	White-eyed Vireo	<u>White-winged Crossbill</u>
SHOREBIRDS		
Black-necked Stilt	Mountain Plover	Sanderling
American Oystercatcher	Wandering Tattler	Purple Sandpiper
Black Oystercatcher	Greater Yellowlegs	Buff-breasted Sandpiper
Snowy Plover	Eskimo Curlew	Short-billed Dowitcher
Common Ringed Plover	Surfbird	Long-billed Dowitcher
WATERFOWL		
Ross's Goose	Cinnamon Teal	Black Scoter
Cackling Goose	Harlequin Duck	Barrow's Goldeneye
<u>Canada Goose</u>	<u>Surf Scoter</u>	

CHAPTER 3: ESTIMATING BIASES AND UNCERTAINTY IN THE NESTING PHENOLOGY PREDICTIONS

3.1 Introduction

Two important aspects of any predictive analysis are to determine whether the method introduces biases, and to provide estimates of uncertainty concerning the predictions. In this chapter, simulations were used to first determine whether the use of backcalculation (Chapter 1) leads to biases in the analytical approach (Chapter 2), and whether these are important when predicting nesting phenology (Panels 4 and 5 of Part 2 – *Species Accounts*). To complete the topic, the use of backcalculated data was also compared to the use of nest observations raw data with no backcalculation.

The uncertainty associated with the nesting phenology predictions was investigated by estimating the number of days by which predicted dates were expected to differ from the “true” dates using simulations. Using this estimate of uncertainty, a map was developed for each species showing two confidence levels associated with the predictions: one for an area of interpolation, where sufficient data were available to reach an adequate level of confidence in the prediction, and one for an area of extrapolation, where greater caution is advised.

3.2 Determining the effect of backcalculation

The initial intention behind the codification of the backcalculation algorithms in the *rNest* package was to calculate the full chronology of all nest records. This was to provide a better estimate of the proportion of active nests at different times over the breeding season (Chapter 1). This is in contrast to establishing a nesting phenology based on the use of raw nest record data, which are often limited to nest observation made during a single visit. Whether this is justified and whether this leads to biases when predicting nesting phenology is discussed in this section.

Does backcalculation lead to biases in predicting nesting phenology?

The backcalculation algorithms were designed to place most nest observations in the middle of their corresponding nesting stage, independent of the date of observation. For example, if a nest record comprises a single observation and the number of eggs reported corresponds to the

estimated clutch size, the observation is positioned in the middle of the incubation period. For nest visits made at the beginning of the nesting season, it is expected that a greater proportion of observations classified in the incubation stage will, in reality, have been made at the beginning of the incubation stage. Consequently, the algorithms are expected to produce biased estimates for the earliest first egg dates. This is because all early season nest observations classified in the incubation stage may in reality have been made at the beginning of incubation, but are nonetheless placed in the middle of that stage. Thus, the use of backcalculated data to infer the earliest first egg dates may lead to an “early” bias, where the earliest first egg dates estimated through backcalculation tend to be earlier than their true dates (Figure 3.1). The same holds true for the latest first egg dates, as observations made later in the season and classified as being in the incubation stage, may have a greater probability of having been made at the end of the incubation stage. This creates a “late” bias when inferring the latest first egg dates from backcalculated data. The same reasoning applies to nest departure dates estimated through backcalculation. Overall, it was expected that the backcalculation procedure would introduce an “early” bias when estimating the beginning of the nesting period and a “late” bias when estimating the end of the nesting period.

Relying only on actual nest observation dates may also provide biased estimates of first egg or nest departure dates. For example, if first egg dates are determined using only the observations of eggs, the first egg dates may be estimated later than the true dates, as all nest observations with eggs will have been made at or later than the true first egg date. Thus, contrary to the “early” bias associated with backcalculations, a “late” bias is expected when estimating the beginning of the nesting season, or first egg dates, using only nest observations (Figure 3.1). Inversely, an “early” bias is expected if using only nest observations to estimate nest departure dates, where as there is a “late” bias associated with the use of backcalculations. Simulations were used to determine the magnitude of these biases. These were restricted to the study of first egg dates, as the results should also be applicable to the estimation of nest departures dates. The importance of the different biases in terms of the number of days is assessed in this section.

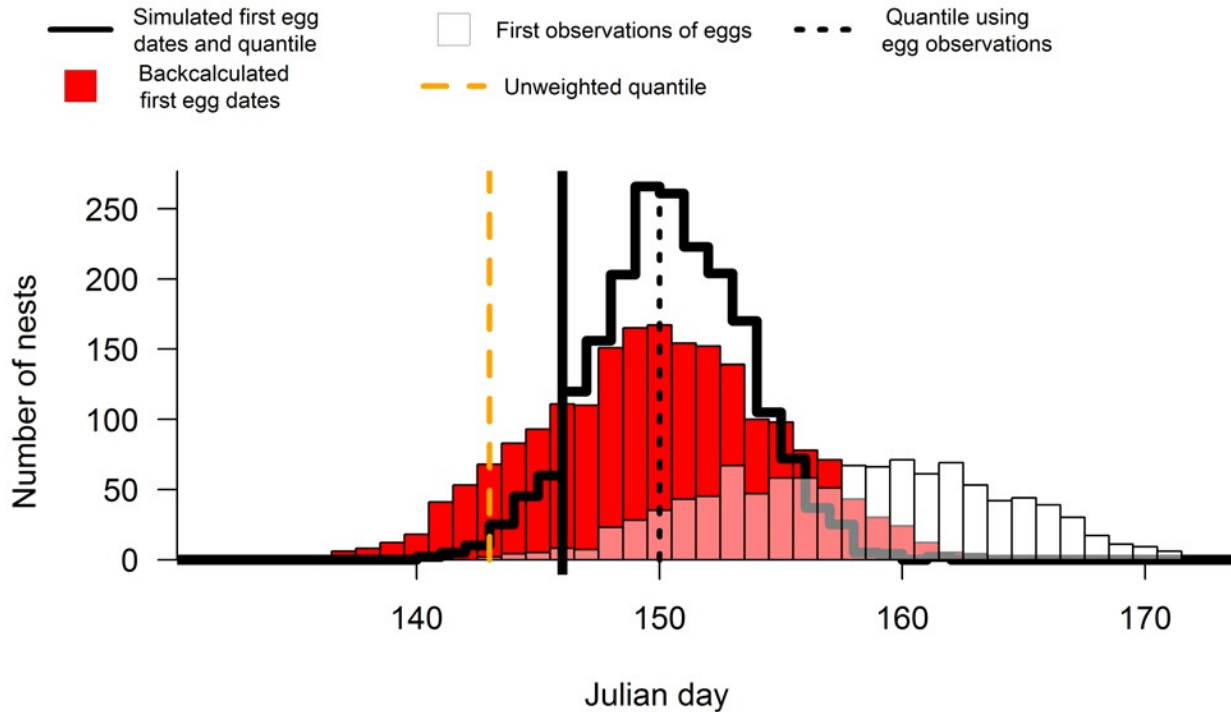


Figure 3.1. “Early” or “late” biases resulting from estimating first egg dates using backcalculated first egg dates or the first observation of eggs only, respectively. The quantile estimated is 10% in both cases. The theoretical population contained 1,000 nests and was constructed by simulating 1,000 first egg dates according to a normal distribution centered on Julian day 150, with a standard deviation of 8 days. The distribution of backcalculated first egg dates was obtained by randomly selecting a single observation from each simulated nest.

Theoretical populations of 1,000 nests with known nest chronologies were simulated using first egg dates generated according to a normal distribution. Each theoretical nest chronology was constructed using a simulated first egg date, and specific nesting parameters representative of Canadian species were used for each simulated population. For each nest in the theoretical set of chronologies, nest observations were randomly selected and the first egg date was estimated using backcalculation. This procedure provided a theoretical distribution of first egg dates which served as a benchmark against which it was possible to compare the distribution of first egg dates estimated through backcalculation, and the distribution of first nest observations with eggs based on estimates using raw data with no backcalculation (Figure 3.1). Because the interest was in determining the bias associated with the estimation of first egg dates, only nests with observations of eggs were considered when building the distribution of first nest observations

with eggs. Unless otherwise stated, the 10% quantile of all generated distributions was used to compare the different estimated quantiles with the theoretical quantile in the simulated population.

Four scenarios were studied to determine if, and how, different variables affected the magnitude of the biases when estimating the 10% quantile of first egg dates. The scenarios in question were the effect of: 1) the temporal concentration of the laying period (Figure 3.2); 2) the duration of the active nesting period, and of the nesting stages, with parameters representative of small-, medium- and large-sized species (Figure 3.3); 3) the distribution of the number of observations per nest, which was used to study the varying level of uncertainty in backcalculations (Figure 3.4); and 4) the specific quantile estimated (Figure 3.5). Each of the above-mentioned figures shows the distribution of the first egg dates in the theoretical population (thick black line), the distribution of the backcalculated first egg dates (red bars), and the distribution of the first observations of eggs (transparent white). The magnitude of the biases is illustrated by the distance of the different quantiles from the theoretical ones. For the different scenarios, the bias is expected to increase with the length of the theoretical active nesting period, as the backcalculation uncertainty increases for species with longer nesting periods. It should also increase as smaller quantiles are selected, because of a more important effect of extreme dates or aberrant data. Conversely, the bias should decrease with an increase in the proportion of chronologies associated with a high level of certainty. There were no clear expectations concerning the effect of the degree of temporal lumping of true first egg dates. This phenomenon occurs at higher latitudes, with the nesting period being generally shorter in the harsher north. It is also observed in late-breeding neotropical migrants, where nesting tends to be more synchronous across their range.

In addition to the quantile using the first observations of eggs (black dotted line), four other quantiles (based on backcalculated first egg dates) were used to study the magnitude of the potential biases. The tested quantiles were associated with a different weighting method and/or the use of different data. The additional quantiles were: 1) a quantile weighted by the proportion of the backcalculation uncertainty relative to the length of the active period (one of the weighting factors used in Chapter 2 for the modelling of nesting phenology; red line); 2) a quantile weighted by the multiplicative inverse of the backcalculation uncertainty (dark red dotted line);

3) an unweighted quantile using all backcalculated nest records (orange dashed line); and 4) an unweighted quantile using only those nests backcalculated with the greatest degree of certainty (including observations of laying, hatching or departure from nest; blue dashed line). Concerning the anticipated results for the different quantiles, the unweighted quantile based on nests backcalculated with the greatest certainty should be the least biased, as there should be less backcalculation uncertainty associated with this. By contrast, the unweighted quantile using all nest records should be the most biased, as it does not give a greater importance to nest records backcalculated with the greatest degree of certainty. Between the two weighted quantiles, the one using the multiplicative inverse of the backcalculation uncertainty should be the least biased, as it gives more importance to nest records backcalculated with the greatest degree of certainty. The low bias of this weighted quantile should be similar to the unweighted quantile using only nests backcalculated with the greatest certainty.

As expected, for all scenarios, the 10% quantile of first egg dates estimated using egg observation dates from the raw data had a “late” bias (black dotted line), which was generally of greater magnitude than the one associated with backcalculated data (Figs. 3.2 to 3.5).

Conversely, when there was a bias, the quantiles based on backcalculated data had an “early” bias. All scenarios had a varying degree of bias associated, except for the one based solely on nests with the greatest certainty concerning dates (blue dashed line) (Figs. 3.2 to 3.5). The two weighted quantiles were generally less biased than the unweighted one (orange dashed line) and the one using egg observations (black dashed line). Furthermore, the quantile weighted using the multiplicative inverse of the backcalculation uncertainty generally had the least bias of the four (dark red dotted line). For backcalculated data, the bias tended to be greater when the timing of laying was more synchronized (Figure 3.2); when species had long active nesting periods (Figure 3.3); when there was generally a smaller number of observations per nest (Figure 3.4); and when smaller quantiles were estimated (Figure 3.5). When using the quantile based on egg observations, the bias also tends to be greater with an increase in the duration of the nesting period and a decrease in the number of observations per nest. However, it tended to decrease when laying was more synchronized, which places the majority of nests within a shorter time period, and when smaller quantiles were estimated. Because nest observations were randomly drawn from each nest, it is important to bear in mind that the simulations used assumed that there was no bias in the temporal pattern of visits to the nest.

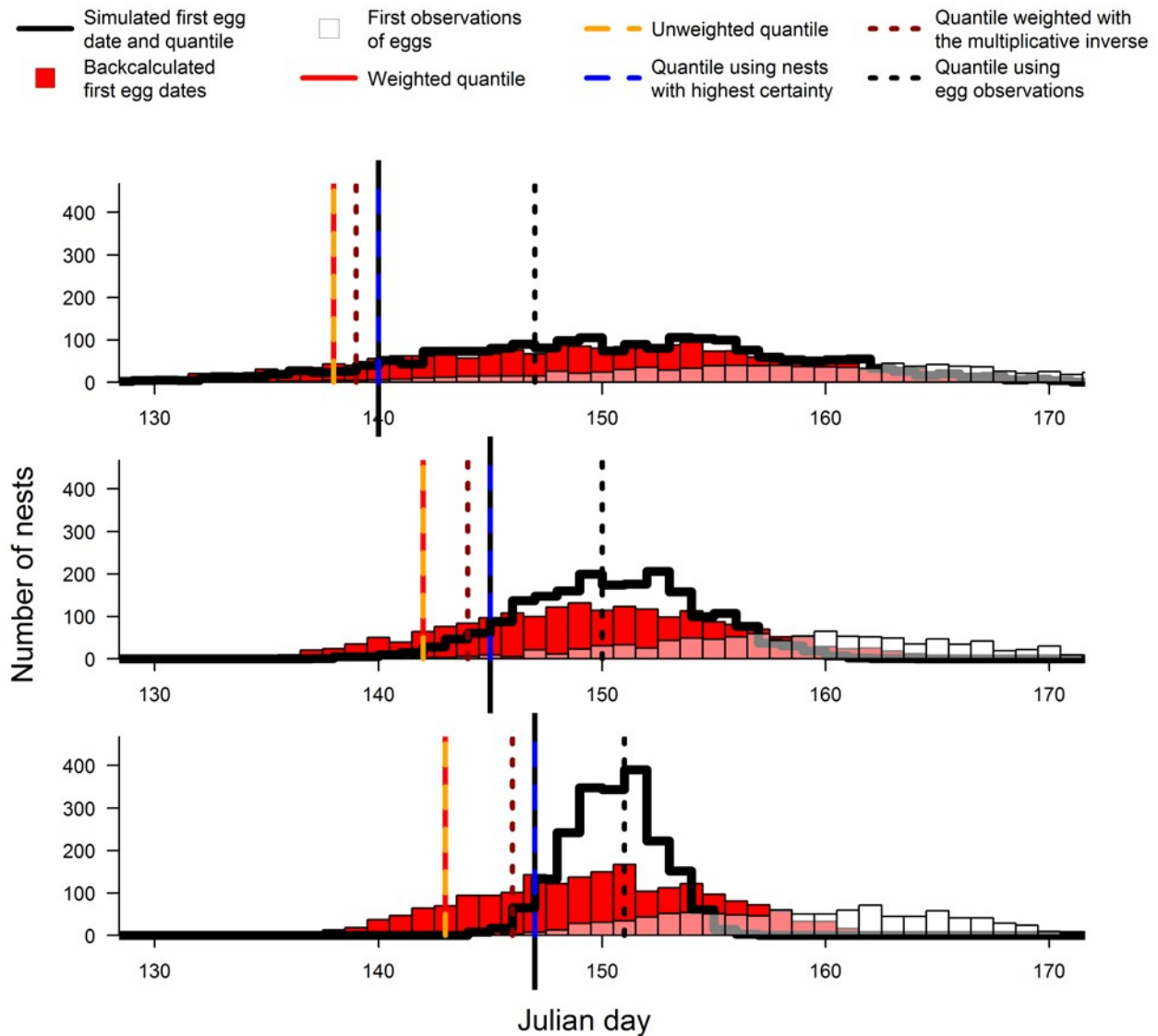


Figure 3.2. Effect of the temporal concentration of the laying period on the bias when estimating the 10% quantile of first egg dates using the first observation of eggs only, or four different quantiles based on backcalculated first egg dates. The theoretical first egg date distributions were simulated according to a normal distribution centered on Julian day 150, with decreasing standard deviation of 8 (top), 4 (middle) and 2 (bottom) days. The nesting parameters used to generate simulated nests were: clutch size = 5 eggs, incubation = 15 days and rearing = 20 days. All backcalculated first egg dates were obtained using a single randomly selected nest observation. Note that bicoloured lines indicate overlapping quantiles.

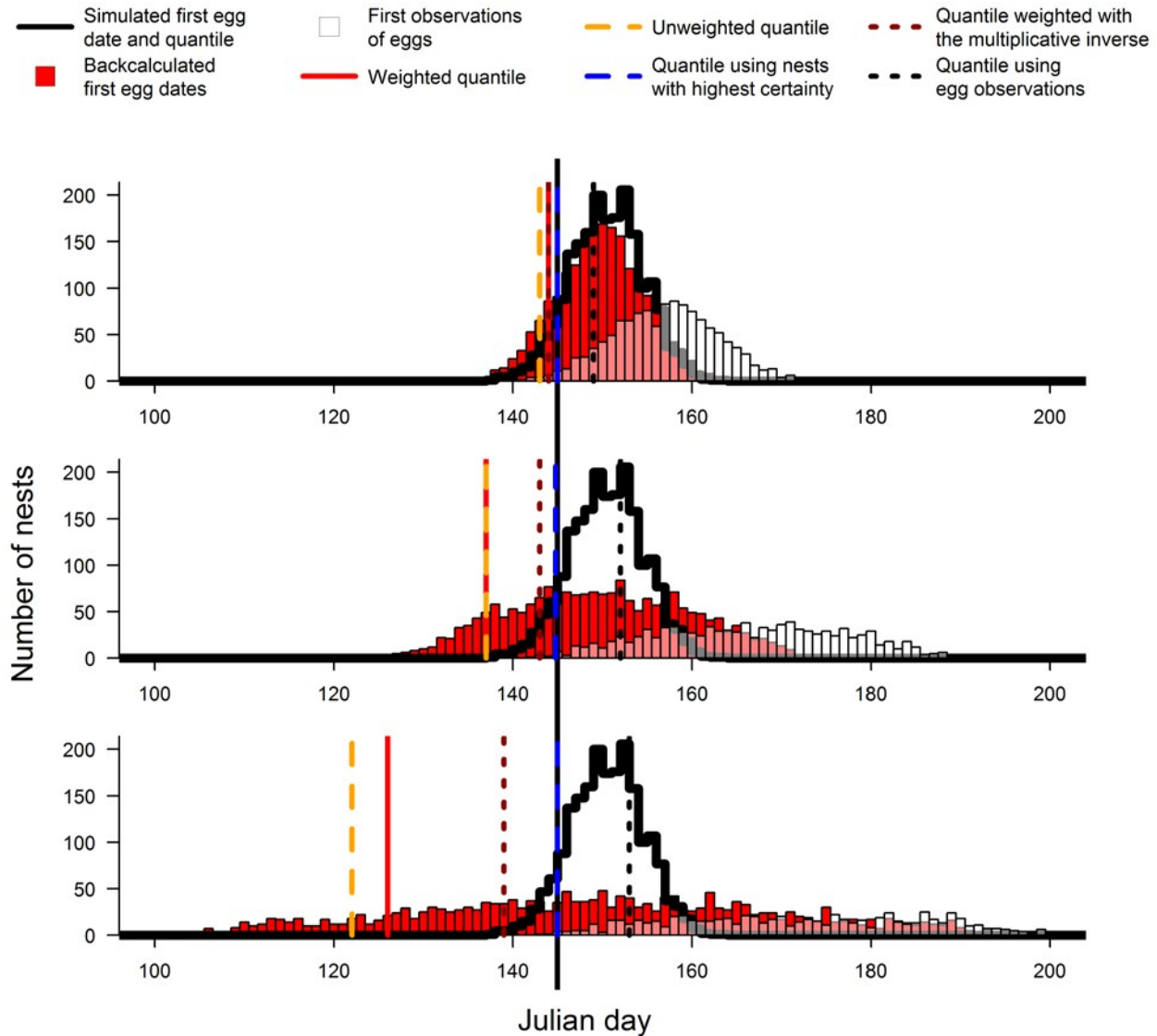


Figure 3.3. Effect of the duration of the active nesting period and of the nesting stages on the bias when estimating the 10% quantile of first egg dates using the first observations of eggs only, or four different quantiles based on backcalculated first egg dates. The nesting parameters used to generate simulated nests were representative of small-, medium- and large-sized species, and were clutch size = 5 eggs, incubation = 11 days (top), 30 days (middle) or 40 days (bottom); and rearing = 10 days (top), 35 days (middle) or 80 days (bottom). The theoretical first egg date distribution was simulated according to a normal distribution centered on Julian day 150, with a standard deviation of 5 days. All backcalculated first egg dates were obtained using a single randomly selected nest observation. Note that bicoloured lines indicate overlapping quantiles.

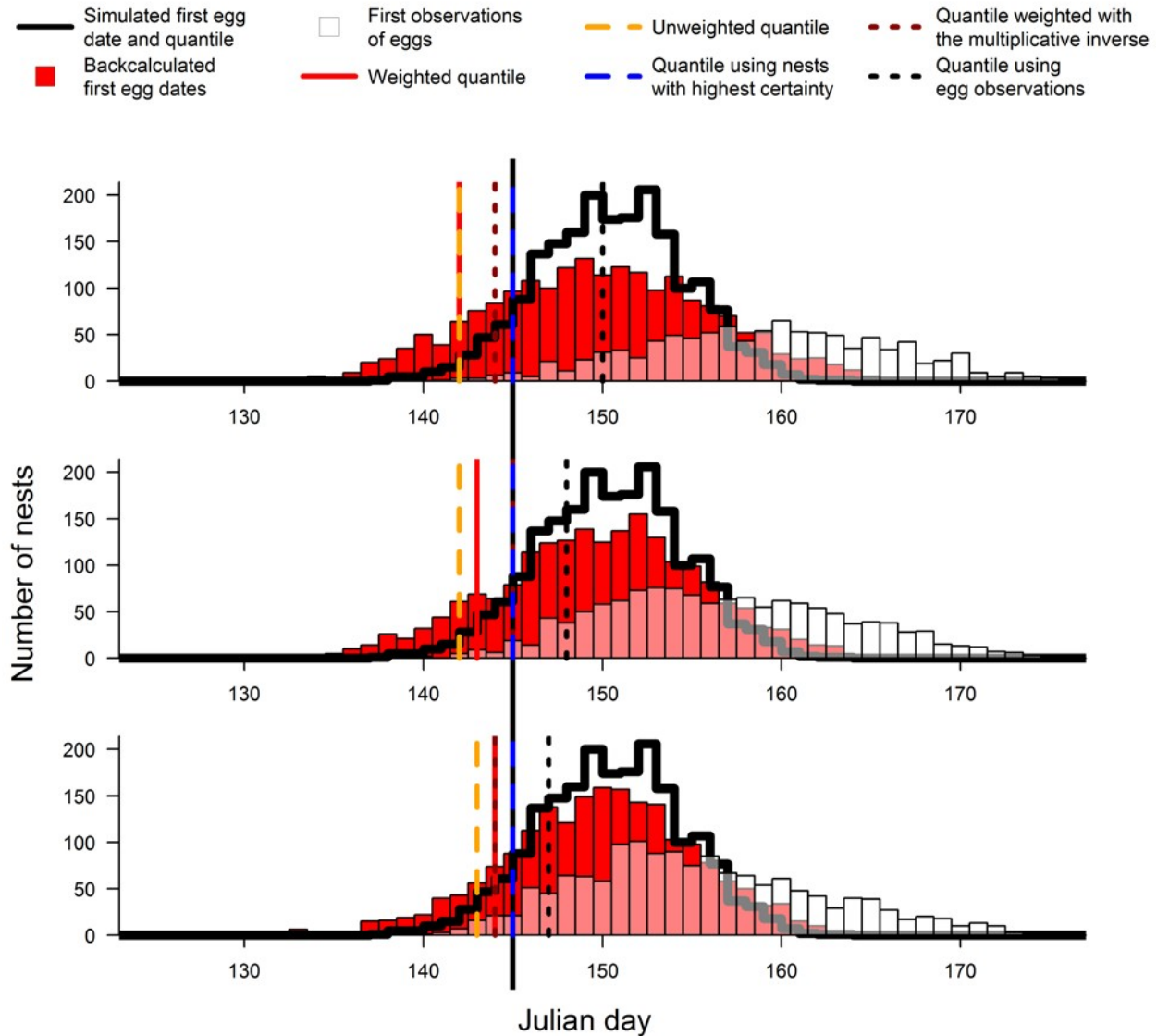


Figure 3.4. Effect of the distribution of the number of observations per nest on the bias when estimating the 10% quantile of first egg dates using the first observations of eggs only, or four different quantiles based on backcalculated first egg dates. The number of nest observations randomly drawn from each nest were 1 (top), 3 (middle) and 20 observations (bottom), and these numbers had the following respective probabilities of being chosen: (1, 0, 0), (0.7, 0.2, 0.1) and (0.5, 0.3, 0.2). The varying number of observations per nest was used to produce a pattern of uncertainty in the backcalculations. The nesting parameters used to generate simulated nests were: clutch size = 5 eggs, incubation = 30 days and rearing = 35 days. The theoretical first egg date distribution was simulated according to a normal distribution centered on Julian day 150, with a standard deviation of 5 days. Note that bicoloured lines indicate overlapping quantiles.

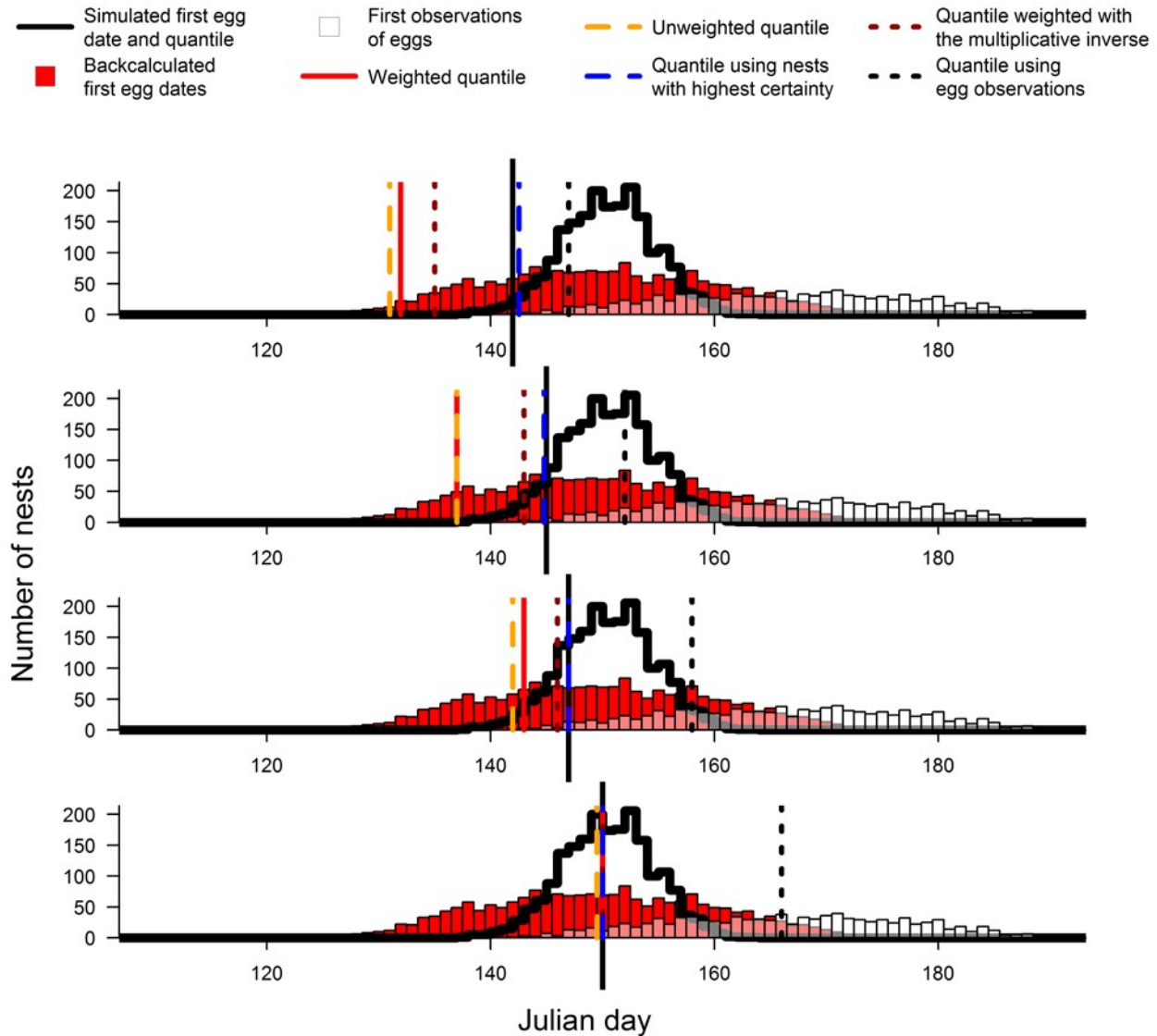


Figure 3.5. Effect of the specific quantile estimated on the bias when estimating first egg dates using the first observation of eggs only, and four different types of quantiles based on backcalculated first egg dates. The quantiles estimated were 2% (top), 10% (upper middle), 25% (lower middle) and 50% (bottom). The nesting parameters used to generate simulated nests were clutch size = 5 eggs, incubation = 30 days and rearing = 35 days. The theoretical first egg date distribution was simulated according to a normal distribution centered on Julian day 150, with a standard deviation of 5 days. All backcalculated first egg dates were obtained using a single randomly selected nest observation. Note that bicoloured lines indicate overlapping quantiles.

The quantile based on nest records backcalculated with the greatest certainty and the weighted quantile using the multiplicative inverse of the backcalculation uncertainty showed no bias, or a much lower levels of bias than the weighted quantile with the proportion of the backcalculation uncertainty relative to the length of the active period, which is the weighting factor used for the modelling in Chapter 2. This was expected as both give a much greater influence to nesting dates estimated with greater certainty. However, because of this, both quantiles also considerably reduce the effective sample size, and so, predictions are made using a smaller number of nests records. When fewer observations are available, the greater influence given to certain nests can have an important impact on the prediction curves and confidence intervals, increasing the uncertainty surrounding predictions (see Section 3.4). Therefore, a certain compromise has to be made between the potential bias generated and the uncertainty in providing acceptable predictions. It seems more appropriate and useful to have predictions that are slightly early, but more precise, than to have predictions that are less biased, but which could be much further from the true values, due to the lower precision associated with a smaller sample size.

Another way of reducing the bias might be to opt for a quantile larger than the 10% quantile for first egg dates used in the current report, and a quantile smaller than the 90% quantile for nest departure dates. However, using different quantiles would also exclude a greater portion of early and late nest records and thus represent a smaller portion of the nesting season. This would be more appropriate if the aim was to describe the core nesting period, rather than the whole season. Thus, when the aim is to describe the entire nesting season, as in the present report, a compromise must be made between reducing the bias by using larger quantiles for first egg dates and smaller quantiles for nest departure dates, and covering the majority of the nesting season. It appears more useful to have predictions based on the 10% quantile that are slightly early and the 90% quantile for nest departure dates that are slightly late, rather than using less biased, but more restrictive, quantiles that also exclude a larger portion of the nesting season. On the other hand, as the bias appears to decrease with the use of smaller quantiles for first egg dates when using nest observations, a smaller quantile based on observations, or a larger one for nest departure dates, could be used to portray the whole nesting season. However, estimating more extreme quantiles also requires larger data sets to obtain precise estimates, and erroneous or aberrant nest observations may also have a greater impact on their estimation.

In conclusion, the simulations used suggest that it is hard to eliminate bias when describing the beginning and the end of the nesting season using quantiles, although this can be mitigated for by using appropriate weighting factors when estimating quantiles from nest records. Because the bias is dependent on several factors, it appears difficult to systematically correct for it, especially since the “real” distribution of first egg dates for each species remains unknown, and the pattern of backcalculation uncertainty likely varies between species. However, if the bias associated with using smaller quantiles (e.g., 2%, Figure 3.5) is excluded, the most important bias is associated with species with long active nesting periods. Therefore, as the vast majority of species included in this report have relatively short active nesting periods (median incubation period of 15 days; median rearing period of 14 days, excluding precocial species), the bias may be small for most species, and may often be negligible compared to the uncertainty in the nesting phenology predictions. From a precautionary point of view, an “early” bias is considered acceptable if it slightly overestimates the length of the nesting season, as the longer nesting period predicted would increase the period during which nest protection measures are needed.

How much does backcalculation affect predictions of nesting phenology in the current study?

The models presented cover a wide range of species, each with a different nesting ecology and a different pattern of nest observations. Thus, the bias in predictions may vary across species and this needed to be assessed to determine if the nesting phenology predictions presented are reliable. One important result from the previous section is that the quantiles using only nest records backcalculated with the greatest degree of certainty, and the quantiles weighted with the multiplicative inverse of the backcalculation uncertainty, provided the least biased estimates. Therefore, the importance of the bias in the system presented can be assessed by comparing predictions derived using both of these methods, with predictions derived from the method of prediction presented in this report, which uses the weighted quantiles with the proportion of the backcalculation uncertainty relative to the length of the active period. If the bias associated with the use of backcalculation is large, predictions made using the method employed in this report should be generally much earlier for first egg dates, and much later for nest departure dates, than predictions derived from the two less biased methods. Instead of comparing the three types of predictions for all species, the exercise can be validly restricted to species for which the greatest

biases are expected, such as those with long active nesting period (e.g., the Bald Eagle), species with temporally concentrated nesting seasons (e.g., late-nesting neotropical migrants), and species with a low proportion of nests backcalculated with a high degree of certainty (e.g., raptors). By comparing the different predictions using species for which the most important biases are expected, it is possible to obtain an idea of the maximal biases encountered within the presented system and to decide whether adjustments need to be made when providing nesting phenology predictions.

The comparison between model predictions for a selection of species for which the greatest degree of bias was expected is shown in Figure 3.6. Comparisons were restricted to species for which there were at least 40 nests available for the predictions based on nests with of the greatest backcalculation certainty. The top row shows the four usable species with the longest active nesting periods (i.e., Bald Eagle (BAEA) = 120 days, Osprey (OSPR) = 94 days, Great Blue Heron (GBHE) = 89 days and Red-tailed Hawk (RTHA) = 81 days). The middle row shows a random selection of four late-nesting, long distance migrants that show a relatively synchronous laying period (i.e., Least Bittern (LEBI), Indigo Bunting (INBU), Wood Thrush (WOTH) and Common Tern (COTE)). The bottom row shows the four usable species with the smallest proportion of nests with the maximum degree of backcalculation certainty (i.e, Ferruginous Hawk (FEHA) = 3%, Mountain Chickadee (MOCH) = 8%, Red-breasted Nuthatch (RBNU) = 8% and White-crowned Sparrow (WCSP) = 9%). In addition, species with the longest active nesting periods (first row) also showed a relatively small proportion of nests with a maximum degree of backcalculation certainty (10%, 13%, 16% and 10%, respectively). By comparison, the mean proportion of nests with the maximum degree of backcalculation certainty for all species modelled is approximately 26% (Figure 3.7).

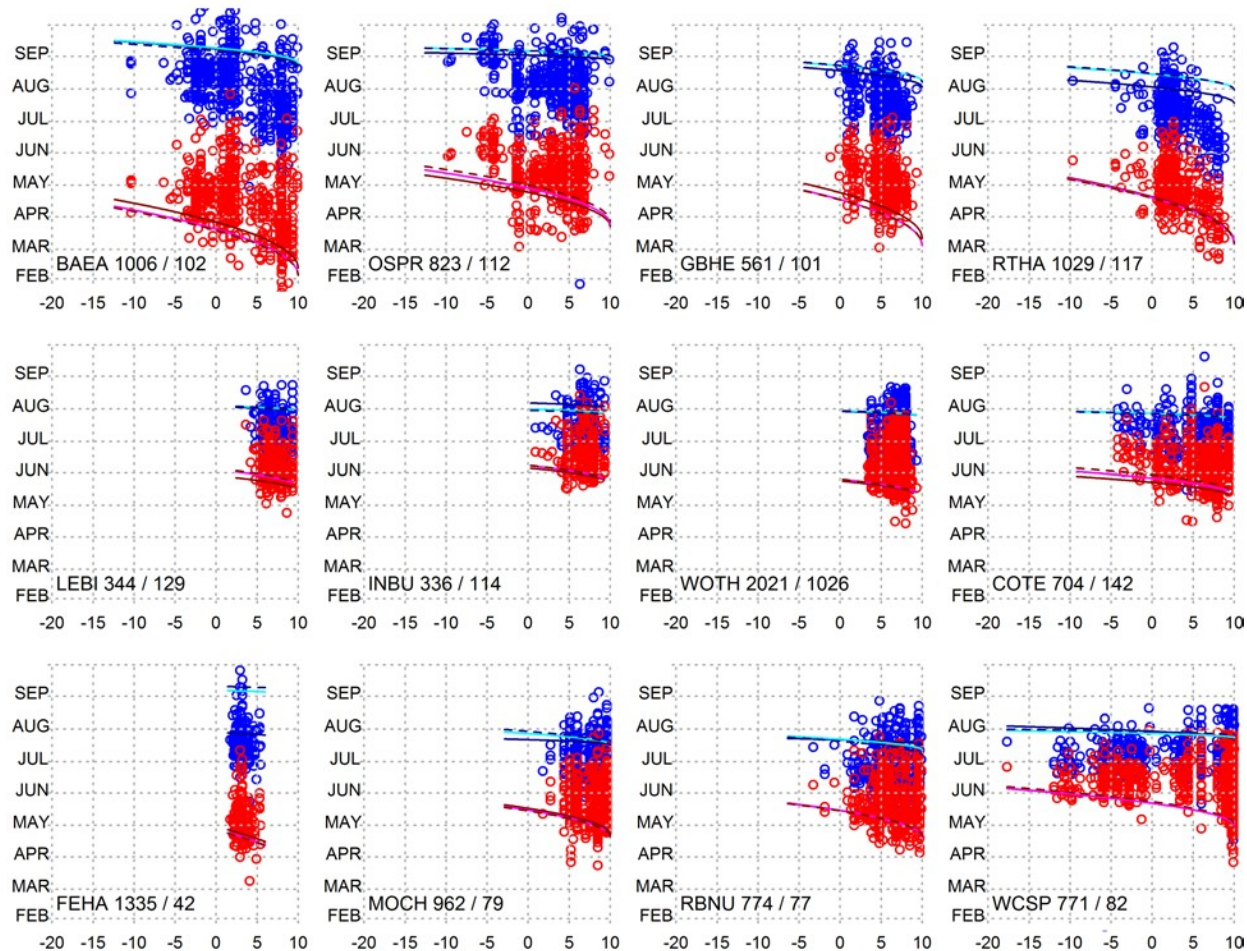


Figure 3.6. Comparison of a selection of species showing predictions derived using the weighted quantiles with the proportion of the backcalculation uncertainty relative to the length of the active period (red and blue solid lines); the multiplicative inverse weighting method (magenta and turquoise solid lines); or the nest records with chronologies backcalculated with the greatest certainty (red and blue dashed lines). The x axis represent the mean annual temperature in Celsius and the y axis the date. The 4-letter code for each species is given in the lower left-hand corner of each graph (see previous pages for full name of species). The numbers that appear after the code represent the total number of nests used and the numbers of nests with the highest degree of certainty (including laying, hatching or departure from nest observations), respectively. The difference between the two numbers gives an idea of the reduction in effective sample size when using the multiplicative inverse weighting.

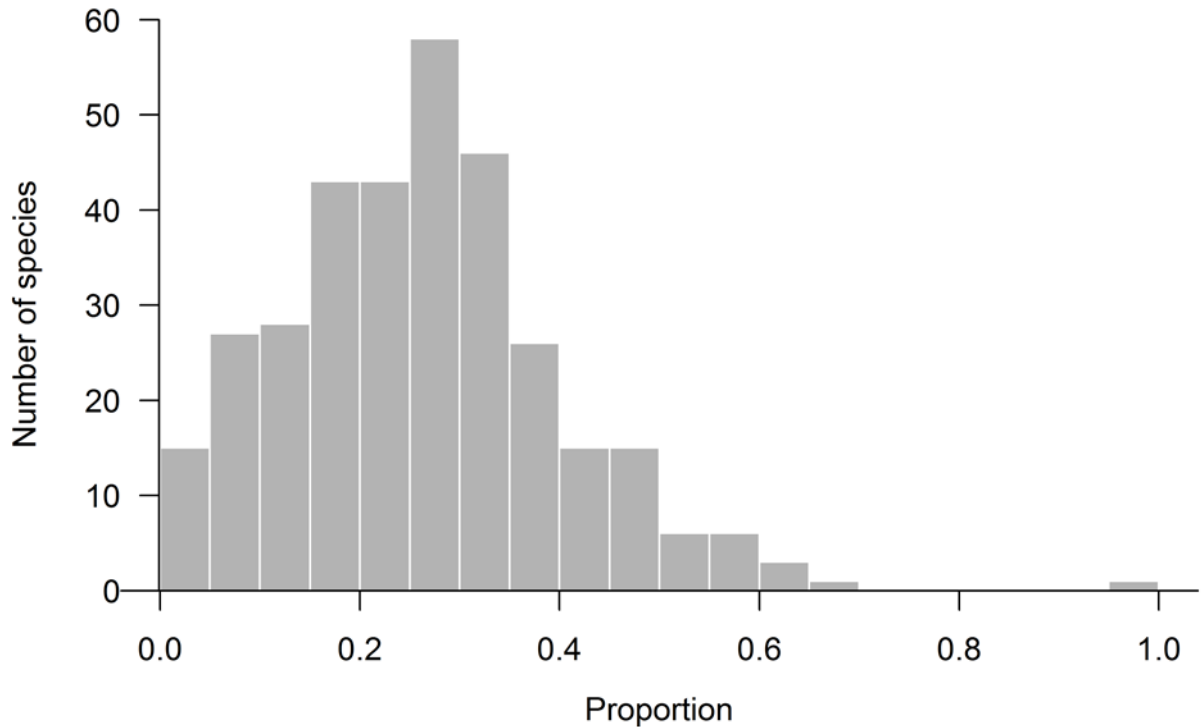


Figure 3.7. Distribution in number of species of the proportion per species of nests backcalculated with the highest degree of backcalculation certainty (including laying, hatching or departure of nest observations) (mean = 26%). All species modelled are included (n = 311).

The comparisons showed that, in general, the bias may not be as important as that suggested by the simulations. For species with the longest active nesting period (top row), for which the bias was expected to be the highest, the predictions using the least biased method were even earlier for first egg dates, and were similar or later for nest departures dates. Indeed, if there were biases associated with using backcalculation for these species, they had little effect on the predicted nesting period. Where predictions appear especially early or late, this may instead be due to erroneous status codes (e.g., fledged eagles reported with status code “young” even though they were outside the nest, which would have been interpreted as being in the rearing period). The bias appeared more systematic in the case of late nesting neotropical migrants (middle row), for which predicted first egg dates were always earlier using the method retained for this report. The difference was, however, generally small and no longer than five days. The difference also appeared to be less important in the case of nest departure dates. Finally, there seemed to be no

systematic bias for the species for which there were few nests estimated with a high degree of certainty (bottom row). There was a large difference in nest departure predictions for the Ferruginous Hawk, which may be due to the low number of observations with a high degree of certainty; however, the difference is the opposite of that expected. Thus, although a bias was apparent in certain cases, this was generally sufficiently small to allow the production of reliable and useful predictions. Moreover, it should be remembered that for the overwhelming majority of modelled species the bias should be small or even negligible compared to the uncertainty associated with predictions.

Another argument for using backcalculation in the method employed in this report, rather than a more severe weighting method, is that the reduced effective sample size resulting from severe weightings for certain species is often quite small, which would inevitably lead to more uncertainty in the estimation of prediction curves for these species. Moreover, the pattern of uncertainty for a given species may not be random across regions. This is because nests coming from certain regions may have been followed with a greater degree of effort. In certain cases, this could give more influence to the regions in question in the estimation of the prediction curves, since nests from regions that lacked certainty would have been discarded, or would have had a much reduced influence. The greater influence of certain regions may still be a problem with the weighting method used in this report, but discarding more nests would likely exacerbate the problem. Therefore, for most species, the use of predictions based solely on nest chronologies with a high degree of certainty would likely lead to greater uncertainty in predictions, because these species may not have sufficient remaining data to produce reliable predictions. Figure 3.8 shows comparisons between confidence intervals obtained through the current weighting method and the multiplicative inverse method for a random set of species (top row: Chestnut-sided Warbler (CSWA), Great Horned Owl (GHOW), Common Redpoll (CORE), Northern Harrier (NOHA); middle row: Yellow-breasted Chat (YBCH), Great Gray Owl (GGOW), Red-bellied Woodpecker (RBWO), and Ruffed Grouse (RUGR); and bottom row: Willow Flycatcher (WIFL), Bullock's Oriole (BUOR), European Starling (EUST), and Cape May Warbler (CMWA)).

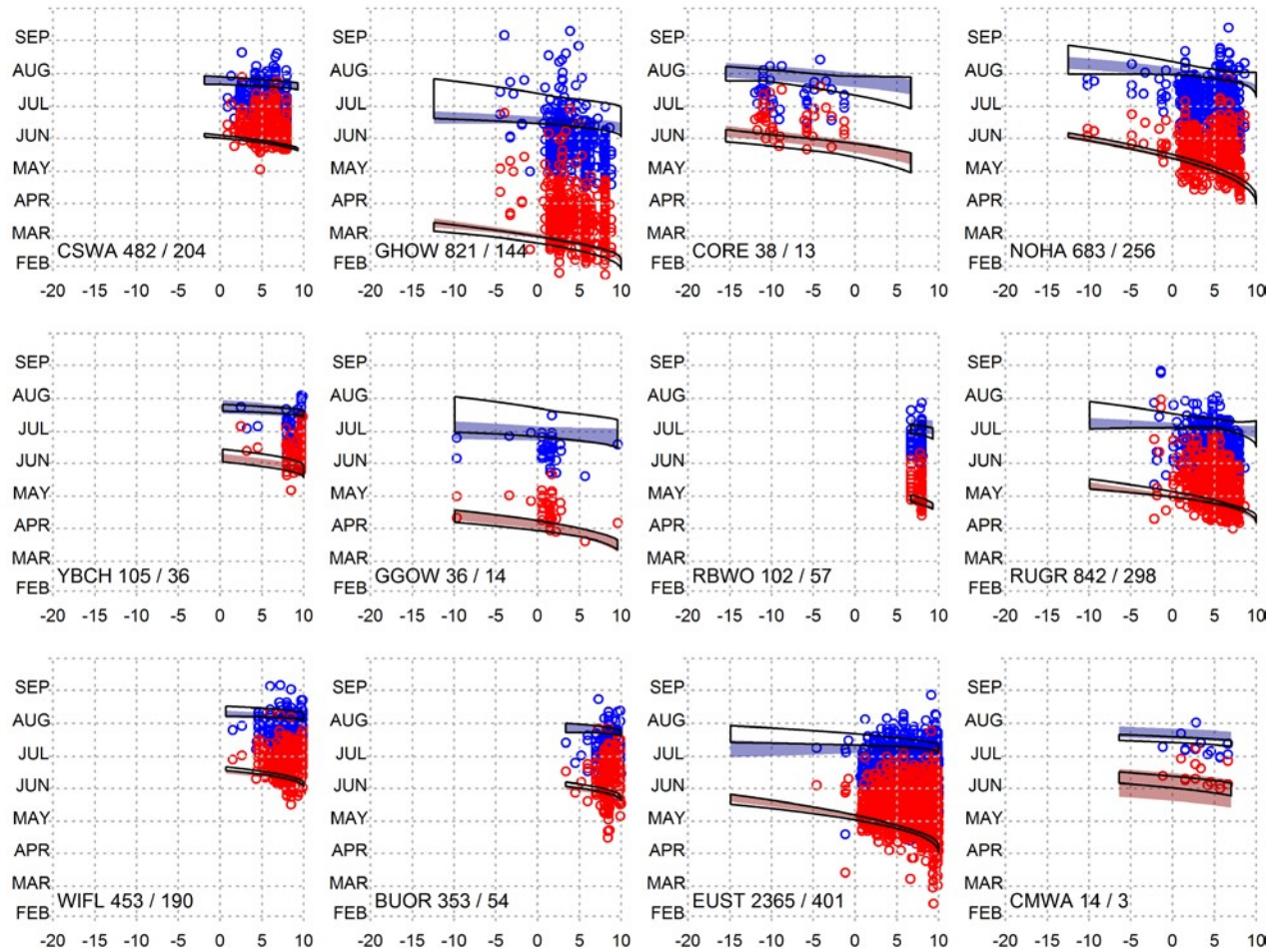


Figure 3.8. A random set of species showing the comparison between confidence intervals using observations weighted either with the percentage of uncertainty relative to the length of the active period (colored intervals), or with the multiplicative inverse of the backcalculation uncertainty (transparent intervals). The x axis represents the mean annual temperature in Celsius and the y axis, the date. The 4-letter code for each species is given in the lower left-hand corner of each graph (see previous pages for full name of species). The numbers that appear after the code represent the total number of nests used and the numbers of nests with the highest degree of certainty (including laying, hatching or departure from nest observations), respectively. The difference between the two numbers gives an idea of the reduction in effective sample size when using the multiplicative inverse weighting.

In most cases, the confidence intervals were much larger for the multiplicative inverse method, which is probably due to the reduced effective sample size, and thus a greater uncertainty in predictions. The difference was also more pronounced for species that were associated with grouping variables with few species. In conclusion, the bias in predictions appeared to be generally small using the backcalculation method based on records weighted with the proportion

of uncertainty relative to the length of the active period, even for species with a long active nest period. Therefore, this method was kept, rather than, the two others that seemed to produce less reliable results. A bias which slightly extends the nesting period also seems more in accordance with a precautionary approach to nest conservation and protection.

When predictions for first egg dates appear unacceptably early for a given species, or nest departure dates appear unacceptably late, it is more likely due to problems in model fitting, with temporal or spatial correlation in the data, or erroneous status code (e.g., fledged eagles reported with status code “young” even though they were outside nest, which would have been interpreted as being in the rearing period, or records of unhatched eggs at the end of the season lacking status codes indicative of egg failure).

Estimating the proportion of active nests without the use of backcalculation

As mentioned in the previous section, the use of raw data from nest observations may introduce a “late” bias when trying to estimate the beginning of the nesting season and an “early” bias when estimating the end of the nesting season, which may underestimate the actual length of the nesting season. Simulations were used to determine how the quantiles based on nest observations were related to the proportion of active nests. As expected, these showed that the use of nest observations may wrongly estimate the true first egg and/or nest departure dates, as the date for the 25% quantile of the first observation of eggs corresponds to a moment when about 55% of nests are already active (Figure 3.9). Likewise, the proportion of nests still active on the date for the 75% quantile of the last observation of young is approximately 60%. However, the discrepancy between the quantiles used for nest observations and the proportion of active nests will likely depend on the same variables that affect the bias when using backcalculation. The simulations suggested that caution is needed when describing the nesting period using nest observations, with the aim of indirectly obtaining an idea of the proportion of active nests. This is because the quantile of nest observations always wrongly estimates by a certain number of days the same quantile in the proportion of active nests. However, the bias may not always be as important as that shown in the simulations in Figure 3.9, as it may be affected by a number of different elements. Considering that the bias is more important when using larger quantiles for first egg dates, the bias may be reduced by opting for a smaller quantile when using nest observations, or a larger one for nest departure dates.

One way to estimate the proportion of active nests from nest observations would be to simply multiply the proportion of nest observations on each day by the length of the active period (Figure 3.10). Indeed, if observations are randomly made by observers during the active period, the probability of obtaining a nest observation on a given day along the active period of a nest is the multiplicative inverse of the length of the active period ($1 / \text{length}$). Thus, for a set of nests, the proportion of active nests on a given day is given by the proportion of nest observations multiplied by the length of the active period and divided by the mean number of observations per nest (or the ratio between the number of nest observations and the number of nests). Because of sampling variability, the number of nest observations will vary between days, producing a ragged pattern. Modelling using flexible curves (e.g., GAMs) can be used to smooth the daily values obtained and evaluate the proportion of active nests for each day (Figure 3.10). However, this method requires that nest observations are made randomly over the active period. If nest observations are biased toward a certain period, the estimated distribution of active nests will be biased. A large number of nests would also probably be required to obtain reliable estimates of the proportion of active nests. Therefore, although this method provides another way of describing the nesting phenology that does not rely on backcalculations, it relies on the assumption that the number of nest observations should be independent of the nesting stages, which may not be the case.

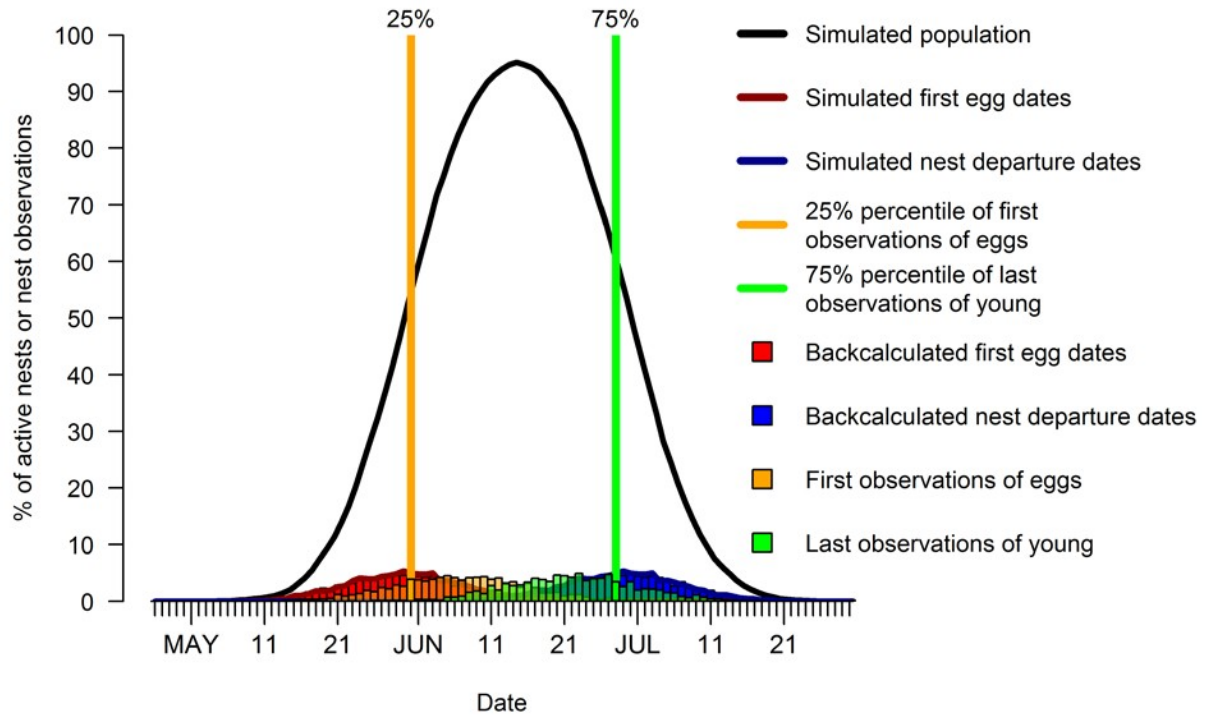


Figure 3.9. Simulation showing how the estimates of the 25% quantile (percentile) of the first observation of eggs and the 75% quantile of the last observation of young is related to the proportion of active nests. The two estimated quantiles correspond, respectively, to a moment when about 55% of nests are already active or when about 60% of nests are still active. A single randomly selected observation per nest was used. The theoretical population was generated using 1,000 simulated first egg dates drawn from a normal distribution centered on Julian date 150, with a standard deviation of 8 days. Nesting parameters used to generate nest chronologies were clutch size = 4 eggs, incubation = 13 days and rearing = 15 days.

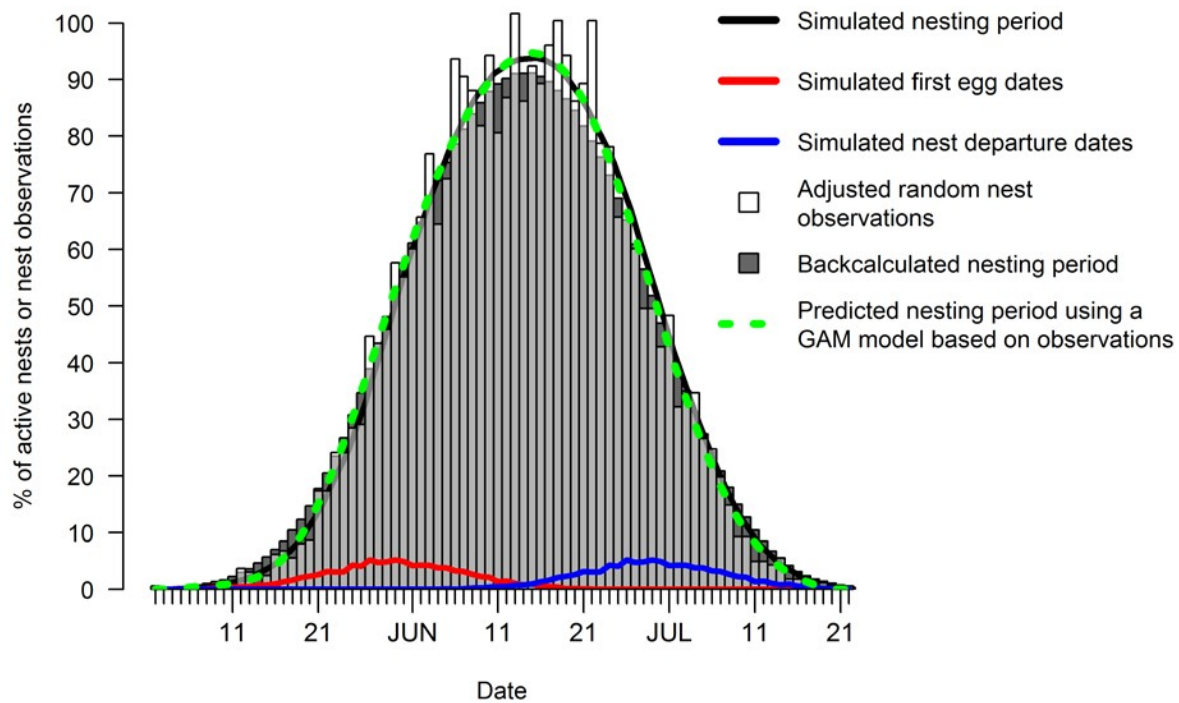


Figure 3.10. Comparison between the patterns of nesting activity produced using backcalculated data (dark gray) or nest observations only (transparent white) using a simulated population of 1,000 nests. The black line shows the proportion of active nests in the simulated population from which nest observations were drawn. The red line shows the proportion of first eggs laid and the blue line shows the proportion of departures of the last young on each day. The dark gray bars show the proportion of active nests from backcalculated nest observations. The transparent white bars show the daily proportion of nest observations multiplied by the length of the active period for the simulated species. The simulated population had nesting parameters corresponding to the American Robin (clutch size = 4 eggs, incubation period = 13 days, and rearing period within the nest = 15 days). (The number of observations per nest was 1, 5 or 20 observations and these numbers were respectively selected with the probabilities 0.7, 0.2 and 0.1.) Nest observations were drawn randomly from nest records. The dotted green line shows predictions for the proportion of active nests from a general adaptive model using the proportion of nest observations on each day, corrected by the ratio between the number of nest observations and the number of nests. Predicted proportions from the model were adjusted to remain within the $[0, 1]$ interval.

3.3 Estimating the regional uncertainty in predictions of nesting phenology

The two most important factors contributing to the uncertainty associated with predicting nesting phenology are the natural variability across nest chronologies and sample sizes. Predictions will have greater precision for species with a more synchronous nesting season among individuals (e.g., late-breeding neotropical migrants) or those with a larger nest record sample size (Figure 3.11). Moreover, for a given species, the different number of nest records from different regions, coupled with the variability in the timing of nesting events between regions, individuals and years, will also contribute to a variable level of uncertainty in the estimations. For several MAT intervals, there were sufficient nest records to allow acceptable predictions of the nesting phenology based on local observations, but in others, the uncertainty around predictions was probably higher due to the fact that fewer data were available. Thus, this variability of uncertainty needed to be addressed for each species. In this section, the relationship between sample size and the precision in nesting phenology predictions is determined, and species- specific measures of uncertainty, derived. This information is then used to provide a level of confidence in the predictions for the different areas of Canada.

Describing uncertainty

There are several ways of investigating the uncertainty surrounding nesting phenology predictions. One method is to use confidence intervals on prediction curves to provide an idea of the level of precision achieved through the modelling process used (see Chapter 2 for the method and Panel 4 of Part 2 – *Species Accounts* for results). However, this approach is dependent on the specific method of analysis and hence subject to all the associated constraints. In the modelling approach used in this study, the intercept of curves is determined at the species level. The slope, however, is much less flexible, because it is determined by all observations within a group of species, and these are in turn defined by the migratory strategy, the tendency to breed early or late, and the capacity to lay multiple clutches. Therefore, because of the influence of the grouping variables on the effective sample size, the varying number of nest records across the temperature range does not necessarily produce much wider confidence intervals for regions with fewer nest records. Moreover, for a single species, the uncertainty provided by confidence intervals does not take into account the fact that the relationship between the MAT and the nesting phenology might vary across species, even though they are part of the same grouping

variable. However, in this study, the approach of adding confidence intervals to the predicted curves was retained as it remains a relevant means of expressing some of the overall uncertainty associated with the predicted dates.

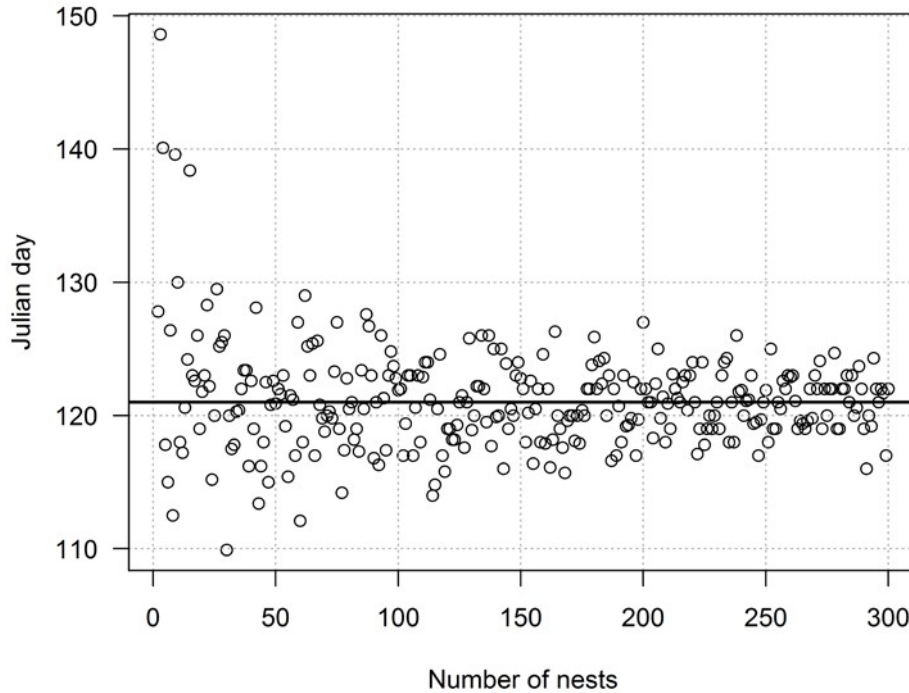


Figure 3.11. Estimation of the date by which 10% of first eggs of the Song Sparrow are or will be laid in relation to sample size. Dots are estimated dates using different sample sizes of nests randomly chosen within the database and the solid line shows the estimated date using all 4,588 nests available.

A prediction independent approach was also developed in the present study to estimate the uncertainty around the predictions. This method examined the uncertainty due to the variability and the amount of data. This can be done by simply resampling nests within the dataset and evaluating the variability across samples. For example, if 100 random samples of 50 nests of a given species were taken from a specific region and the 10% quantile of the first egg date calculated for each sample, it is possible to calculate the standard deviation of the estimation for each sample. Using the set of 100 standard deviations, the expected standard error (ESE) can be estimated by calculating the mean of the standard deviations. This value can then be used to estimate the expected deviation in the number of days between the prediction and the “real” estimated date (e.g., the date on which 10% of first eggs are laid). As the length of the nesting period differs between species and across regions, ESEs are expected to be dependent on the species and the regions of interest, as well as on the sample sizes available in the dataset.

Estimating the uncertainty for each species due to the variability and the amount of data

To produce a reasonable estimate of the ESE as a function of sample size, a large number of nest records are needed to reduce the risk of a potential bias due to a specific set of nesting dates that are not representative of the phenology of the species. If only a few nest records are available, the standard deviation estimated by resampling within those nests will be strongly biased toward the dates reported within the dataset. Moreover, because of the resampling procedure, the standard deviations will also be influenced if there are a limited number of nest records, as the same nesting dates will be resampled several times. Hence, the precision in estimating the variation of the ESE linked to sample size is higher when there are a larger number of nest records to sample from. Similarly, measures of ESE may vary across regions due to the variability in nesting phenology. Because of these factors, for several regions there were insufficient nest records to obtain region-specific estimates of ESE. As the nesting season is expected to be longer in southern Canada and most of the available nest records are from the south, it is possible to build conservative estimates of ESE as a function of sample size using nest records from the south. These estimates of ESE can then be used as upper limits of uncertainty for colder regions, where the variability in the nesting phenology between individuals of a given species is likely to be smaller due to the shorter nesting season.

In the present report, the ESE was estimated for all species having at least 100 nest records. It was assumed that 100 nests would provide sufficient variability to produce adequate estimates of ESE when resampling. For each species, 30 samples (using a resampling with replacement approach) were taken for each sample size ranging from 2 to 50 nests, producing a total of 1,470 samples for each species. For each sample, the three dates used to describe the nesting phenology were calculated: the date by which 10% of first eggs would have been laid, the nesting midpoint (50%), and the date by which 90% of nests would have been vacated.

Generalized additive models (GAM) with specification for a smoothing factor, with five knots for anchoring the resulting curves, were used to describe the relationship between sample size and ESE for each species, and for each date describing the nesting phenology. More specifically, species, nesting phenology descriptors (i.e., first egg, nesting midpoint and nest departure) and

sample size were used as explanatory variables, and the ESE as the response variable.

The relationship established between sample size and ESE (Steps 1 and 2, Figure 3.12) was used to calculate the number of nests required to be able to predict the nesting phenology with an ESE of ± 10 days for each species (Step 3, Figure 3.13). Estimates of the required sample size for nest departure dates were used because they were the highest, and therefore the most conservative in terms of uncertainty. This value was then used to establish the MAT intervals, across Canada, in which predictions were expected to be within 10 days of the “true” dates that were being estimated (Steps 6 and 7, Figures 3.14 and 3.15). Specifically, each 2 °C MAT class with a sufficient number of nests to reach an ESE of ± 10 days was identified (Step 6, Figure 3.14). The highest and the lowest MAT values obtained from these classes were then used to determine the interpolation area by selecting all ecodistricts with a MAT value within this range (Step 7, Figure 3.15). Using this approach, an ecodistrict could be included in the interpolation area even if the number of nest records from it was not sufficient to reach an ESE of ± 10 days.

The interpolation area thus formed was described as the area (corresponding to a MAT range) where the predictions were expected to be within ± 10 days of the “true” dates. Predictions in the area outside the interpolation area (or MAT range) had the greatest degree of uncertainty. Another way of presenting this is to consider that in ecodistricts within the MAT range that had sufficient data (allowing for an estimate with an ESE of ± 10 days) were “interpolated”, whereas elsewhere they were “extrapolated”. Thus, greater caution is advised when using species-specific predictions in extrapolated areas.

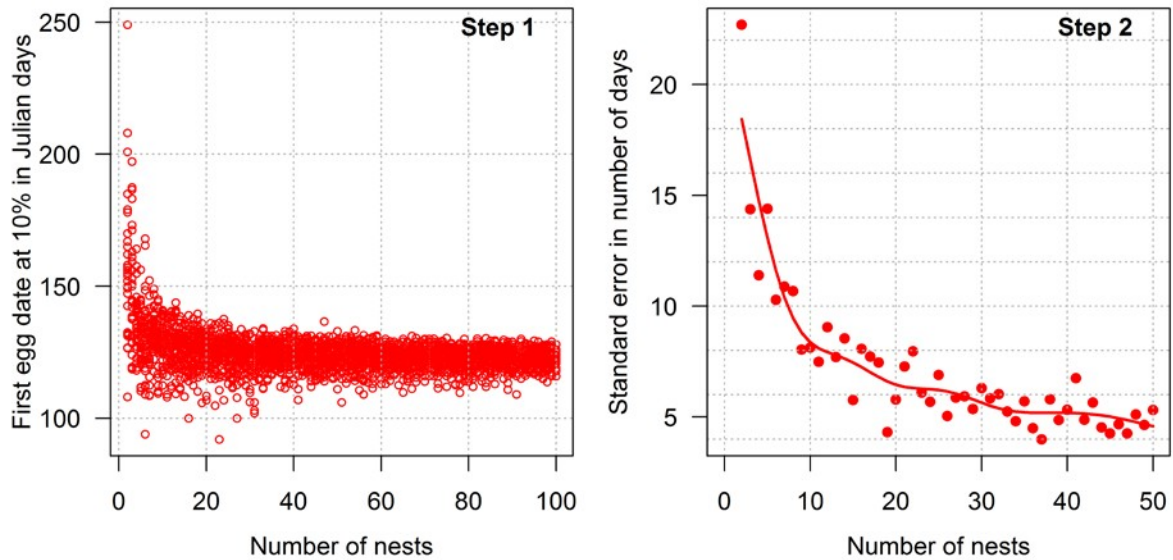
Among the 311 species for which predictions of the nesting phenology are provided, only 262 had enough nest records (≥ 100) to allow an estimate of the relationship between the ESE and sample size based on the resampling procedure. The production of uncertainty maps for these species therefore required the use of two additional calculation steps to indirectly estimate the number of nests required to reach an ESE of ± 10 days (Steps 4 and 5; Figures 3.13 and 3.14). To do this, the duration of the nesting period was used to indirectly estimate the ESE, as this variable should strongly influence the relationship between uncertainty and sample size. All things being equal, for a given level of precision, a larger sample size should be required to estimate dates that are more widely spread out. For example, if individuals of a species nesting in the Arctic usually lay all their eggs between late May and late June, fewer nest observations

should be required to estimate the date by which 50% of first eggs would have been laid with a precision of ± 10 days. By contrast, the same calculation for a species, such as the American Robin, that can lay eggs from April to July in the south, and that may produce multiple clutches, needs a greater number of observations.

For the calculations, the first stage was to estimate the duration of the nesting period by considering the 10% quantile of the first egg dates and the 90% quantile of the nest departure dates based on the backcalculated data for each species (Step 4, Figure 3.13). A regression was then performed to relate the length of the nesting period to the number of nests required to reach an ESE of ± 10 days for the 262 species for which we were able to obtain this information (≥ 100 records, Step 5, Figure 3.14). The predictions derived from the regression then served to estimate the number of nests required to reach an ESE of ± 10 days for species that had fewer than 100 records. As the correlation between the nesting period and the number of nests required to reach an ESE of ± 10 days was relatively weak, a quantile, rather than linear, regression method was used to estimate the 90% quantile, which provided a conservative estimate of the sample size needed for each species.

Mapping of the interpolation zone provides a different means of representing the uncertainty surrounding the predictions, which is complementary to the addition of the confidence interval to the prediction curves. This approach makes it easy to locate the ecodistricts on the map for which an adequate number of nest records were available and thus the places where the predictions have a higher level of certainty. However, it is important to keep in mind that predictions for ecodistrict in the extrapolation area do not necessarily vary by more than 10 days from the “true” dates. The maps are simply designed to show those parts of the breeding range of a given species for which predictions were supported by fewer data than the minimum required to obtain an ESE of ± 10 days. Although there is higher uncertainty concerning predictions for these regions, many are likely to be very close to the “true” values. Furthermore, because the extrapolation area is generally located further north in colder regions, where the natural variability across nest chronologies is expected to be lower, the number of nests required to reach an ESE of ± 10 days is probably overestimated. Thus, the distinction between the interpolation and the extrapolation areas may not be as important as might be first thought, and the predictions for the latter are nevertheless useful.

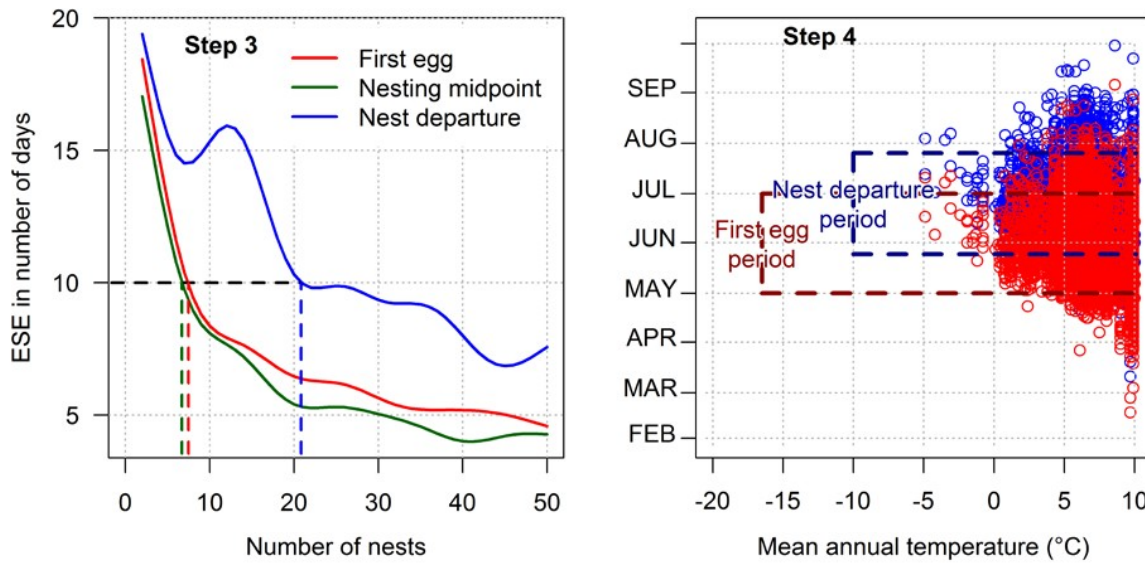
For species in colder regions or with limited breeding ranges, the confidence intervals of the prediction curves may provide a better estimate of uncertainty than simply assuming that predictions may differ by more than 10 days from the ESE. Confidence intervals are probably also more suited for species found across a limited temperature range, or for species nesting more synchronously across Canada, such as neotropical migrants. Another example worth considering is that of the Long-tailed Duck, where no area within its breeding range is considered to have predictions with an ESE of ± 10 days and, consequently, all of the breeding range lies within the extrapolation area. However, even if greater caution is advised when using extrapolated nesting predictions, the variability in nest chronologies across the MAT range is rather small for the Long-tailed Duck, and confidence intervals surrounding the prediction curves might provide a better estimate of the uncertainty concerning the predictions for this species. Finally, because uncertainty maps are based on nest departure date, which seems to be the date of the nesting period that is estimated with the highest uncertainty, the overall uncertainty is likely overestimated for several species. The greater uncertainty in this parameter compared with the first egg date may be due to different factors, such as a right-skewed natural distribution of first egg dates, records of second or replacement clutches later in the nesting season, or problems with the interpretation of nest observations (e.g., abandoned nests with eggs, and young outside the nest reported as young in the nest). A further possible addition to the overestimation of uncertainty was the selection of conservative estimates based on the 90% quantile to obtain a gauge of the sample size needed to reach an ESE of ± 10 days for species with less than 100 nest records. In conclusion, the estimation of uncertainty was established using confidence intervals and the expected standard error, thus providing maximum information for each species when evaluating the quality of the nesting phenology predictions (see Panels 3 and 4 of Part 2 – *Species Accounts*).



Step 1: Variation of the date of the estimated quantiles according to the sample size (number of nests) for the Song Sparrow ($n = 4,588$ nest records). Quantities of 10 %, 50 % and 90 % were calculated for the dates of first egg, nesting midpoint and nest departure, respectively. The values presented show the example of the 10% quantile of the dates for the first egg. This relationship was established only for species with at least 100 nest records.

Step 2: Thirty random samples of Song Sparrow nest records were taken for each of the sample sizes (number of nests) ranging from $n = 2$ to $n = 50$. The standard error was calculated for each sample size, using the blocks of 30 standard deviations obtained from random samples. Values were calculated for each estimated quantile. The values show the example of the 10% quantile for the first egg. For each quantile, a generalized additive model was used to fit a curve to describe the decrease in the expected standard error with sample size.

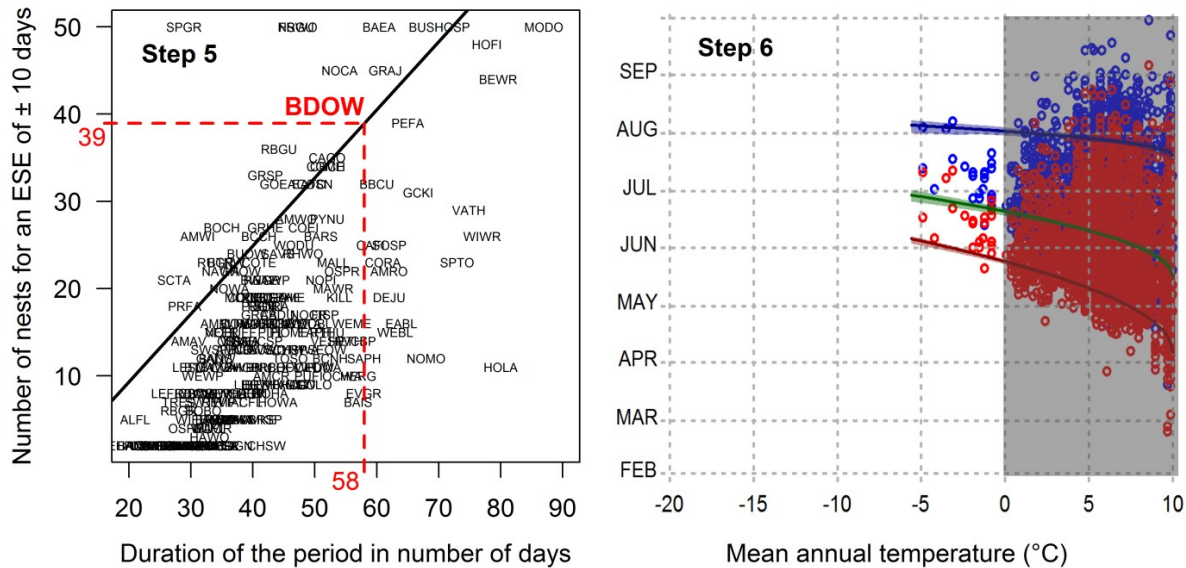
Figure 3.12. Steps 1 and 2 of the ecodistrict identification process where nesting phenology is predicted with an expected standard error of ± 10 days



Step 3: The prediction curves of the expected standard error (ESE) were used to identify the sample size needed to reach an ESE of ± 10 days. The values of the curve associated with the nest departure dates were subsequently used, as these were the highest. In the case of the Song Sparrow, 21 nests were required to reach the desired uncertainty threshold (± 10 days) and to determine the corresponding mean annual temperature range (Step 6). The values for the number of nests are presented in Panel 3 of Part 2 – *Species Accounts*).

Step 4: Additional step to indirectly estimate the number of nests needed to achieve an ESE of ± 10 days for species with fewer than 100 nest records. The duration of the first egg, nesting midpoint and nest departure periods was estimated by respectively considering the 10%, 50% and the 90% quantiles of the dates for each period using all the backcalculated data for each species. The figure shows the example of the Song Sparrow. For clarity, the nesting midpoint dates and the duration of the nesting period are not shown.

Figure 3.13. Steps 3 and 4 of the ecodistrict identification process where nesting phenology is predicted with an expected standard error of ± 10 days

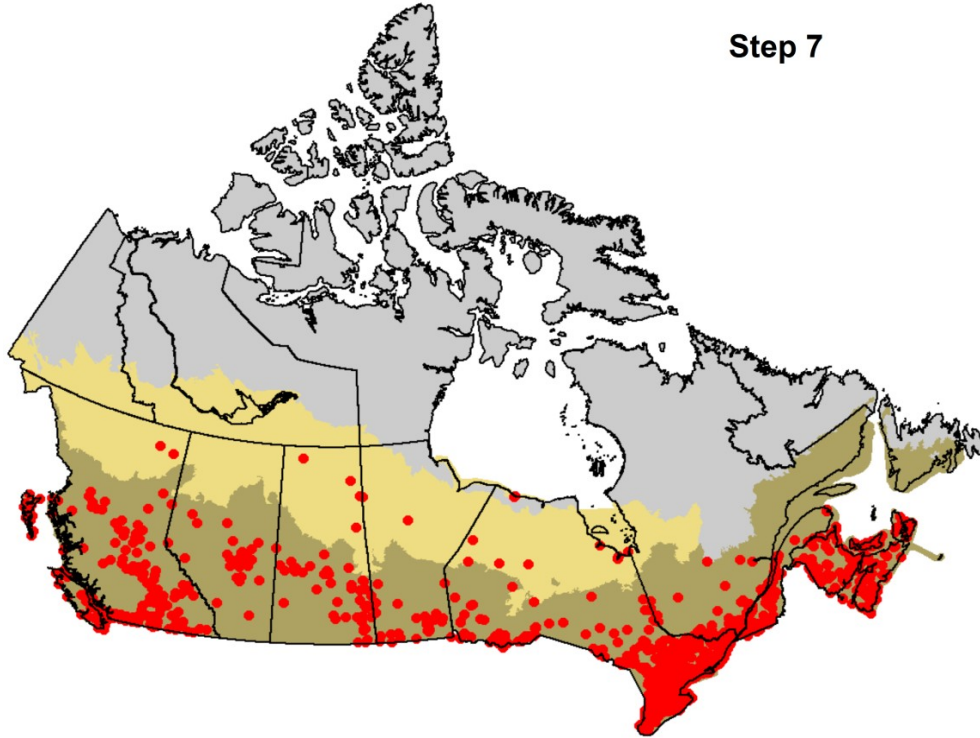


Step 5: Additional step to indirectly estimate the number of nests needed to achieve an expected standard error (ESE) of ± 10 days in species with fewer than 100 nest records. The sample size (number of nests) required to obtain an ESE of ± 10 days (result of Step 3) was plotted as a function of the corresponding duration of the nest departure period (result of Step 4) for all species having at least 100 nest records, and a quantile regression was used to estimate the 90% quantile (black line). This provided a generally conservative estimate of the sample size required to reach an ESE of ± 10 days for all species with less than 100 nest records. The derived value for the Barred Owl (BDOW) is highlighted in red.

Step 6: The interval of mean annual temperature (MAT) classes by 2°C divisions (the shaded area) in which the number of nests (for the Song Sparrow, in this case) was sufficient to reach an expected standard errors of ± 10 days. The red dots are the backcalculated first egg dates and the blue dots are the associated nest departure dates in relation to the MAT. The red line shows the estimated dates at which 10% of first eggs would have been laid in relation to the MAT, the green line shows the estimated nesting midpoint dates, at which 50% of nests had reached the middle of their active period, and the blue line shows the estimated nest departure dates when 90% of young would have left the nest.

Figure 3.14. Steps 5 and 6 of the ecodistrict identification process where nesting phenology is predicted with an expected standard error of ± 10 days

Step 7



Step 7: All ecodistricts with mean annual temperatures (MAT) values comprised within the range determined in step 6 were used to establish an area within the breeding range of the species (shown here for the Song Sparrow) in which each nesting phenology prediction were within an expected standard error of ± 10 days. Predictions for ecodistricts inside this area (dark brown) are considered to be “interpolated”, and predictions for ecodistricts outside of this area (light brown) are considered to be “extrapolated”, and are associated with a lower level of confidence. The red dots show the locations of the nest records used in the models. For other species, see maps in Panel 3 of Part 2 – *Species Accounts*.

Figure 3.15. Step 7 of the ecodistrict identification process where nesting phenology is predicted with an expected standard error of ± 10 days

CHAPTER 4: REGIONAL NESTING CALENDARS FOR MIGRATORY BIRDS

4.1 Introduction

In 2016, the Canada-United States Migratory Birds Convention celebrated its 100th anniversary. As a result of this treaty, in 1917, Canada adopted a law that today is known as the *Migratory Birds Convention Act, 1994* (MBCA). The purpose of this act is to implement the Convention by “*protecting and conserving migratory birds – as populations and individual birds – and their nests*”, anywhere in Canada. To insure the implementation of this protection, technical information about general nesting periods is needed to inform the planning of activities, so that the risk of detrimental effects to federally protected species (designated under the name “*migratory birds*”), their nest and eggs can be reduced. This information has been produced in the past, but the methods used varied considerably across Canada, ranging from professional knowledge, to a variety of statistical examinations of nest records (Taylor *et al.*, 2008; Coulton and Robertson, 2009; Vaillancourt 2010). Current information sharing, and the national scope of some development projects, reinforced the need to provide regional nesting calendars for migratory birds that are nationally consistent and built using a standardized approach. This goal motivated the development of the backcalculation (Chapter 1) and modelling procedures (Chapter 2), resulting in the description of the nesting phenology of individual species across Canada (Part 2 – *Species Accounts*). With this information, it was then possible to develop a multiple species approach to describe the progression of the nesting season of migratory birds, providing regional nesting calendars.

To be most useful, regional nesting calendars should not only indicate the beginning and the end of the nesting period, they should also estimate how the intensity of nesting activity changes over time. Indeed, the variation of nesting intensity over time helps assess when the majority of birds are nesting. In this study, the length and the intensity of the nesting period in the regional calendars were estimated by simply determining the proportion of species actively nesting at any given time over the nesting season. Species-level predictions, derived from the methodology presented in Chapters 1 and 2, were used to determine when a species was considered to be actively nesting, that is, the period between when 10% of first eggs have been laid and when 90% of nests have been vacated. Although this does not provide a direct estimate of the total number of active nests at any given time, it should correlate with the overall intensity of nesting

activity. To be able to give an estimate of the number of active nests would require either a database of unbiased nest records for species and regions, or a detailed account of the abundance of species in different regions and habitats across Canada, along with their relative nesting intensity. To the best of our knowledge, the level of information required to obtain reliable estimates using this kind of analysis is not currently available for all regions of Canada (see also the second consideration in Section 4.3).

Finally, in order to provide a simple and global portrait of the nesting period, “regional” nesting calendars were determined, according to general nesting zones based mainly on MAT, and to increase their applicability, these were also separated into the three main bird habitats (i.e., forest, open and wetland).

4.2 Calculation of the regional nesting period

Regional nesting calendars are multi-species compilations based on the results of single species models presented for broad geographical areas covering the whole of Canada, referred to as “nesting zones”. To describe the general nesting period of migratory birds in a given nesting zone, the proportion of species known to breed in each ecodistrict that were actively nesting was calculated for each day from early March to the end of August.

To build the calendars for a given nesting zone, all the predicted calendars from the ecodistricts contained in the zone were used, and the median date was determined for each proportion of the species actively nesting. For example, to obtain the date at which 20% of species are actively nesting (i.e., either at the beginning or the end of the season) within a zone that contained 10 ecodistricts, the date when 20% of species were nesting for each of the 10 ecodistricts was calculated and the median of these dates was used as the value for the nesting zone. Furthermore, the calculation of the median was weighted according to the surface area of each ecodistrict to account for the relative weight of ecodistricts, which provided a more representative value for the nesting zone. Together, the median dates for all the proportions of species actively nesting circumscribed the predicted nesting period of a given zone. Since the period is based on medians rather than extreme values, it is thus possible that the nesting period starts earlier or ends later in one or more ecodistricts of the nesting zone. The calendars also provide information about extreme values in the form of two markers that show the earliest and latest dates on which a

species was predicted to be nesting in one or more ecodistricts contained within the zone.

Finally, nesting calendars are presented according to three main habitat types, depending on their associated species: forest, open and wetland environments, with the possibility of a given species nesting in more than one of these habitat types.

Establishing nesting zones

The nesting zones were first determined by classifying ecodistricts into five coarse zones. The aim of this initial step was to break down the nesting phenology into manageable units to help account for the wide variations in species diversity across the country. The chosen way of doing this was to consider these variations at the bird conservation region level (BCR; NABCI, 2007; Figure 4.1; Table 4.1). In terms of spatial scale, when compared to the national ecological framework for Canada, BCR limits correspond to ecozone limits (Marshall *et al.*, 1999). This allows large nesting areas to be established, with finer scale boundaries corresponding to those of the ecodistricts (Figure 4.1).

From west to east, the coarse general zones are distributed as follows:

- Zone “A” is located in British Columbia and includes the BCRs of the Northern Pacific Rainforest (BCR 5), the Great Basin (BCR 9) and the Northern Rockies (BCR 10).
- Zone “B” is located in the western part of Canada expanding north from the US border to the north of Yukon and the Northwest Territories, and east from Alaska to the southern part of Manitoba. It includes the BCRs of the Prairie Potholes (BCR 11), the Boreal Taiga Plains (BCR 6) and the Northwestern Interior Forest (BCR 4).
- Zone “C” is located mostly in the eastern part of Canada expanding north from the southern tip of Ontario to the southern border of the Arctic (BCR 3), and east, from Great Bear Lake in the Northwest Territories, to Cape Breton Island in Nova Scotia. It includes the BCRs of the Lower Great Lakes/St. Lawrence Plain (BCR 13), the Boreal Hardwood Transition (BCR 12), the Maritime Provinces’ portion of the Atlantic Northern Forest (BCR 14), and the southern portions of both the Boreal Softwood Shield (BCR 8) and the Taiga Shield and Hudson Plains (BCR 7).
- Zone “D”, originally within the coarse zone “C”, correspond to the northern portion of

the Québec–Labrador Peninsula up to the Arctic ecozone. It descends south to the north of Mistassini Lake and includes part of Hudson Bay, Anticosti Island and Newfoundland. It comprises the northern parts of both the BCRs of the Boreal Softwood Shield (BCR 8) and the Taiga Shield and Hudson Plains (BCR 7), and the Newfoundland portion of the Atlantic Northern Forest (BCR 14). This zone has similar MATs to that of zone "C" (Table 4.1), but is nevertheless distinguished by differences in species diversity and nesting phenology.

- Zone “N” is located in the Arctic part of Canada and it includes the entire area of the BCR of the Arctic Plains and Mountains (BCR 3), which is found in Yukon, the Northwest Territories, Nunavut, Québec and Labrador.

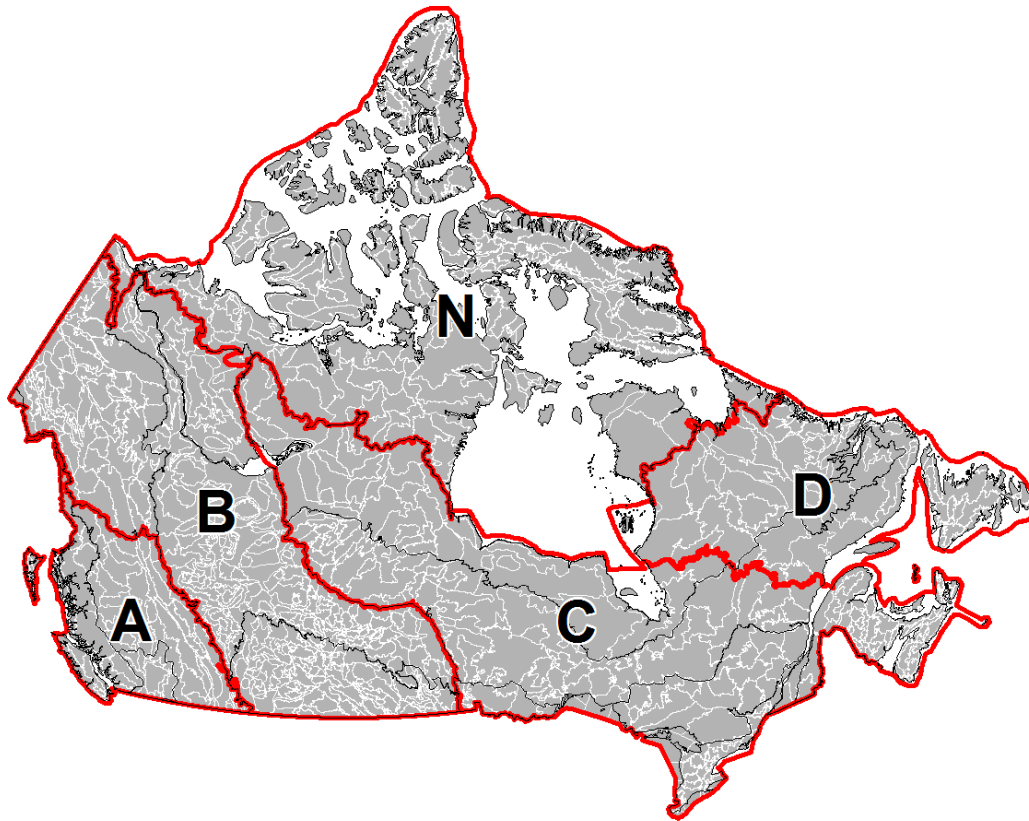


Figure 4.1. First level classification of ecodistricts into five general nesting zones based on assemblages of bird conservation regions (BCR, black lines) and the contours of ecodistricts for the coarse zone “D”. Ecodistricts (pale gray) are shown in the background. See Table 4.1 for the name of each BCR.

Table 4.1. First level classification of ecodistricts (n = 1,021) into five general nesting zones based on Bird Conservation Regions (BCR), and ecodistrict contours in the case of coarse zone “D”. The number (N) of ecodistricts in a zone and the characteristics of the zone, in terms of the minimum (Min) and maximum (Max) mean annual temperature values, and the percent of land surface area in Canada, are shown

Zone	N	Bird conservation region	Min °C	Max °C	Surface Area %
A	86	Northern Pacific Rainforest (BCR 5), Great Basin (BCR 9) and Northern Rockies (BCR 10)	0.7	10	7
B	411	Prairie Potholes (BCR 11), Boreal Taiga Plains (BCR 6) and Northwestern Interior Forest (BCR 4)	-10	6	23
C	245	Lower Great Lakes/St. Lawrence Plain (BCR 13), Boreal Hardwood Transition (BCR 12), Atlantic Northern Forest (BCR 14), and parts of both the Boreal Softwood Shield (BCR 8) and the Taiga Shield and Hudson Plains (BCR 7)	-11.7	9.3	22
D	85	Québec-Labrador and Newfoundland sub-zones of parts of both the Boreal Softwood Shield (BCR 8) and the Taiga Shield and Hudson Plains (BCR 7)	-5.8	5.6	9
N	194	Arctic Plains and Mountains (BCR 3)	-19.9	-3.2	26
No data	17	Ecodistricts with no mean annual temperature (MAT) values	-	-	13

Once the coarse zone were established, ecodistricts were grouped into finer “nesting zones” according to 15 predefined 2 °C MAT intervals ranging from -19.9 °C to 10 °C (Figure 4.2; Table 4.2). Nesting calendars from intermediate zones were also used to determine whether certain areas should be grouped or not, based on the similarities of their nesting calendars. However, in zone B, ecodistricts in B8 and B9 were grouped following a predefined interval of 4 °C to take account of a larger similarity between nesting calendars with variations of MAT. In zone C, ecodistricts in C1 and C2 were grouped using a natural break in the MAT (instead of the predefined intervals), as this provided a better division based on a south (C1: 10 °C to 7.8 °C) to north (C2: 7.5 °C to 6.1 °C) gradient. Ecodistricts in C8 were grouped following a defined interval of 6 °C to obtain a homogeneous nesting zone that was justified by the similarities between their nesting calendars. In zone D, ecodistricts in D3 and D4, which are located in Newfoundland, were merged into one zone and those of D6 (most of Labrador) were grouped following a predefined interval of 4 °C to, again, take account a greater similarity between

nesting calendars with variation of MAT. In coarse zone N, which corresponded to the Arctic region (BCR 3), ecodistricts were grouped following the limits of the ecozones instead of strictly following the predefined MAT classes. This approach was based on the work of Coulton & Robertson (2009) on the nesting phenology of birds in the Canadian Arctic. The three finer zones in the Arctic were: parts of the Southern and Northern Arctic ecozones in Québec and Labrador (N8), which corresponded to MATs between -4 °C and -7.9 °C; the Southern Arctic ecozone (N9; including the part of BCR 3 in Yukon), which corresponded to MATs between -10 °C and -13.9 °C and, in Yukon, to MATs between -8.8 °C and -9.9 °C ($n = 4$ ecodistricts); and the Northern Arctic ecozone (N10; including the Arctic Cordillera), which corresponded to MATs between -19.9 °C and -12.0 °C, but included warmer ecodistricts located at the southern end of Baffin Island around Iqaluit, with MATs between -9.5 °C and -9.8 °C ($n = 17$). Because of very different MAT values compared to the surrounding mainland, the offshore islands of Nunavut situated close to the province of Québec were all excluded from the nesting period calculations. Moreover, all of these islands are grouped in the same ecodistrict, which reduces the value of that MAT for the analysis. However, they were finally associated with the geographically nearest nesting zone. The islands in question were the islands of James Bay including Akimiski Island, which were associated with C6; the Belcher Islands from Long Island to Split Island, which were associated with D7; and the islands of Hudson Bay from Driftwood Island to Smith Island, and Killiniq Island, which were associated with N8. Based on ecozones, Mansel Island and Coats Island were associated with N9, and Akpatok Island, Charles Island, Nottingham Island and Salisbury Island were associated with N10.

Among the 1,021 ecodistricts, 143 were excluded when developing the nesting zones due to the fact that they had no MAT values ($n = 17$) or they exhibited atypical MATs compared to surrounding ecodistricts classified according to predetermined MAT intervals ($n = 126$; Figure 4.2). The latter group included small ecodistricts that were isolated from their predetermined MAT zone, such as warmer northern ecodistricts embedded in a colder nesting zone, and colder southern ecodistricts embedded in a warmer nesting zone. These were excluded based on the general assumption that nesting is initiated gradually from south to north rather than strictly based on MAT. In the Arctic, the use of ecozones to determine finer nesting zones was also problematic because many ecodistricts had atypical MAT values relative to their ecozone. This resulted in the exclusion of 16 ecodistricts, including colder ecodistricts ($\text{MAT} < -14$ °C) in N9

(Southern Arctic), located north of Garry Lake near the Queen Maud Gulf Bird Sanctuary; and warmer ecodistricts (MAT > -14 °C) in N10 (Northern Arctic), located in the coastal area of the Amundsen Gulf from Dolphin Strait and Union Strait to the Prince of Wales Strait, at the southern end of the Northern Arctic ecozone, south of Wager Bay, and on Southampton Island.

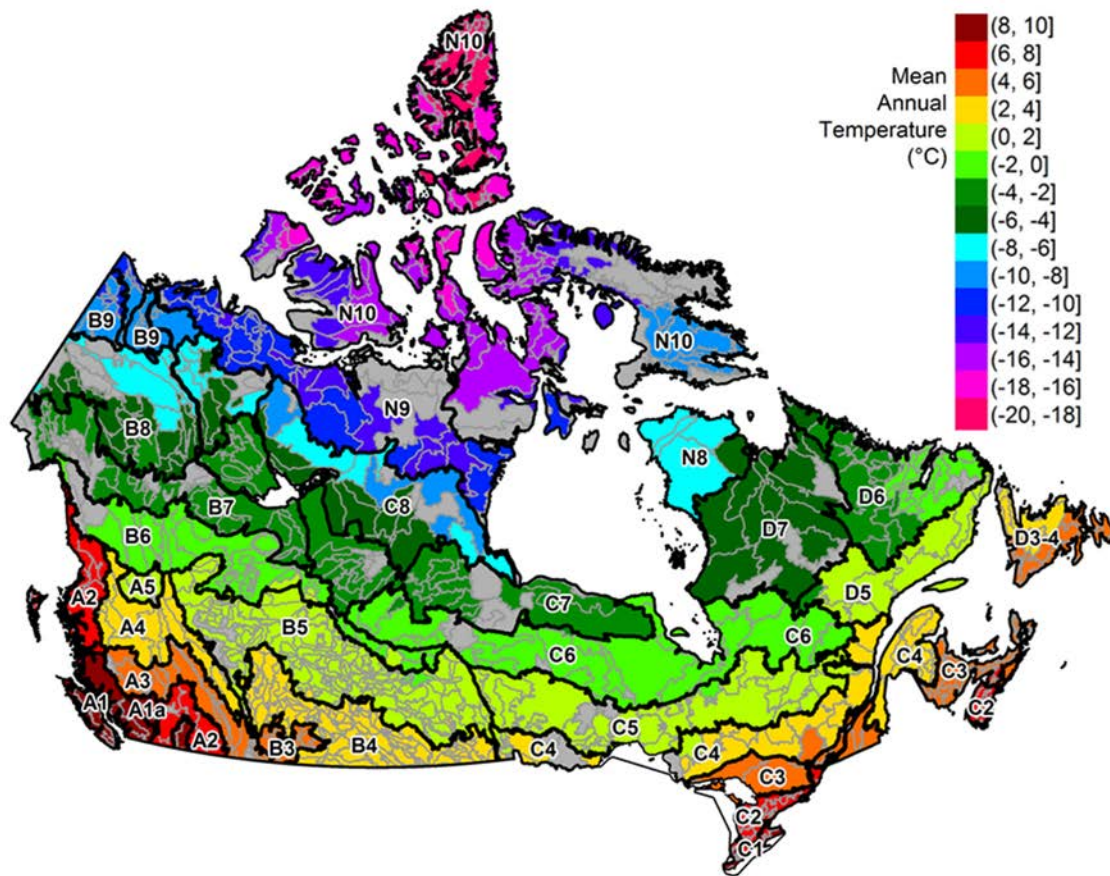


Figure 4.2. Second level classification of ecodistricts into predefined 2 °C –wide mean annual temperature intervals ranging from -19.9 °C to 10 °C. Thick lines show the contours of final nesting zones. Ecodistricts in gray were not considered when building nesting zones because of missing temperature data or because temperature data was divergent when compared to surrounding ecodistricts.

Table 4.2. Second level classification of ecodistricts into predefined 2 °C-wide mean annual temperature (MAT) classes from -19.9 °C to 10 °C, with the minimum (Min) and maximum (Max) MAT values found within each ecodistrict class. Ecodistricts were subsequently regrouped into 27 nesting zones based on the similarities between their nesting phenologies and their proximity. Hence, some nesting zones span a range of MAT greater than 2 °C. Among the 1021 ecodistricts found in Canada, 143 were not considered for the construction of nesting zones because of missing temperature data, or because temperature data was divergent when compared to surrounding ecodistricts. The symbol “]” indicates inclusion of the value and the symbol “(” indicates exclusion of the value

Nesting zone	MAT Class	n	Min °C	Max °C
A1	(8, 10]	14	8.3	10
A2	(6, 8]	16	6.5	8
A3	(4, 6]	19	4.1	6
A4	(2, 4]	18	2.3	4
A5	(0, 2]	3	0.7	1.8
B3	(4, 6]	14	4.1	6
B4	(2, 4]	90	2.1	4
B5	(0, 2]	124	0.1	2
B6	(-2, 0]	39	-1.8	0
B7	(-4, -2]	42	-3.9	-2
B8	(-6, -4]	32	-5.9	-4
B8	(-8, -6]	12	-7.9	-6
B9	(-10, -8]	15	-9.8	-8.8
B9	(-12, -10]	1	-10	-10
C1	(8, 10]	7	7.8	9.3
C2	(6, 8]	25	6.1	7.5
C3	(4, 6]	47	4.2	6
C4	(2, 4]	36	2.1	3.9
C5	(0, 2]	27	0.1	1.8
C6	(-2, 0]	27	-1.9	-0.4
C7	(-4, -2]	29	-3.8	-2.3
C8	(-6, -4]	10	-5.6	-4.2
C8	(-8, -6]	5	-7.4	-6.7
C8	(-10, -8]	4	-9.2	-8
D3-4	(4, 6]	16	4.2	5.6

Nesting zone	MAT Class	n	Min °C	Max °C
D3-4	(2, 4]	7	2.3	4
D5	(0, 2]	10	0.9	2
D6	(-2, 0]	14	-1.8	0
D6	(-4, -2]	12	-3.9	-2.3
D7	(-6, -4]	14	-5.8	-4.1
N8	(-6, -4]	2	-5.8	-4
N8	(-8, -6]	4	-7.6	-6.7
N9	(-10, -8]	4	-9.9	-8.8
N9	(-12, -10]	25	-11.9	-10.2
N9	(-14, -12]	10	-12.6	-12
N10	(-10, -8]	10	-9.8	-9.5
N10	(-14, -12]	17	-13.7	-12.6
N10	(-16, -14]	37	-15.7	-14
N10	(-18, -16]	19	-17.8	-16
N10	(-20, -18]	15	-19.9	-18.1

Species discarded

Among the 364 federally protected species known to breed in Canada, 261 species (72%) were used for the determination of the regional nesting calendars. The species discarded from the modelling process were those lacking data ($n = 87$), those for which the model output was rejected ($n = 10$), and those with an especially early, late or extended nesting season ($n = 6$). With regards to the latter fact, some species such as crossbills can nest almost year-round and it was decided to exclude these from the regional nesting calendars as the aim was to portray the general nesting season. The species excluded because of their atypical nesting period were: Bohemian and Cedar waxwings, Red and White-winged crossbills, Pine Siskin and American Goldfinch. The list of the bird species discarded because of lack of data, or for which the model output was rejected, are shown in Table 2.3 (Chapter 2). Although calendars may not have included all the possible migratory bird species breeding in a given nesting zone, the results are nonetheless representative of the nesting season, as the majority of species were included. Moreover, those federal species not included are likely, at least in part, to breed within the general nesting seasons provided in the calendars. The estimated nesting periods for the species modelled are shown in Panels 4 and 5 of Part 2 – *Species Accounts*.

4.3 Results and Discussion

In Canada, the nesting period of migratory birds varies regionally, due mainly to differences in species assemblages, bioclimatic conditions and habitat type. Figure 4.3 shows the 27 nesting zones and Table 4.3 shows an overview of the estimated nesting periods in third-of-month divisions (early: 1st to 10th of the month; mid-: 11th to 20th of the month; and late: 21st to the end of the month). Based on the migratory birds considered in the regional nesting calendars ($n = 261$ species), the general nesting period may start as early as late March and may extend until the end of August (however, see considerations 1 to 6 below). Following the general trend of the nesting phenology models developed in Chapter 2, the nesting period is delayed in more northerly latitudes, corresponding to harsher climatic conditions (lower MATs), which, for birds, translates to delayed vegetation development and food availability. Specifically, the general nesting period starts in March in southern British Columbia (nesting zone A1) and in Ontario (C1), and becomes gradually later with increasing latitude with nesting starting, for example, at the end of April in breeding zones in the boreal forest (B6, C5, C6, D5), and at the end of May in the

Northern Arctic (N10). However, the general nesting period ends in August for all nesting zones regardless of their location in Canada. From mid-May to mid-August, all nesting zones are predicted to have at least one migratory bird species nesting (Table 4.3).

The estimation of the variation in nesting intensity on any given day is illustrated by the regional calendars (Figures 4.4 to 4.8). The vertical blue bars show the predicted extreme dates for some atypical parts of the nesting area, where nests may be active earlier or later. On average, the nesting intensity gradually increases from the 0% - 5% bracket to the 40% - 60% bracket over the first 29 days (standard deviation (SD) = 8 days) of the nesting period, stays at its maximum intensity ($\geq 60\%$) for 62 days (SD = 6 days), and gradually decrease from the 40% - 60% bracket to the 0% - 5% bracket over the last 25 days (SD = 7 days). The nesting period is longer in the south, extending from March to August, and lasts 149 days in southern Ontario and 141 days in southern British Columbia. It gradually shortens moving north, dropping to a length of 89 days from May to August in the northern part of Yukon and the Northwest Territories (B9), and 86 days in the Northern Arctic (N10). For the whole of Canada, the predictions indicate that the beginning of the intense nesting period, where at least 40% to 60% of species are nesting, extends from the first half of May to the beginning of June. This intense period ends in the second half of July for all regions in Canada (Figures 4.4 to 4.8).

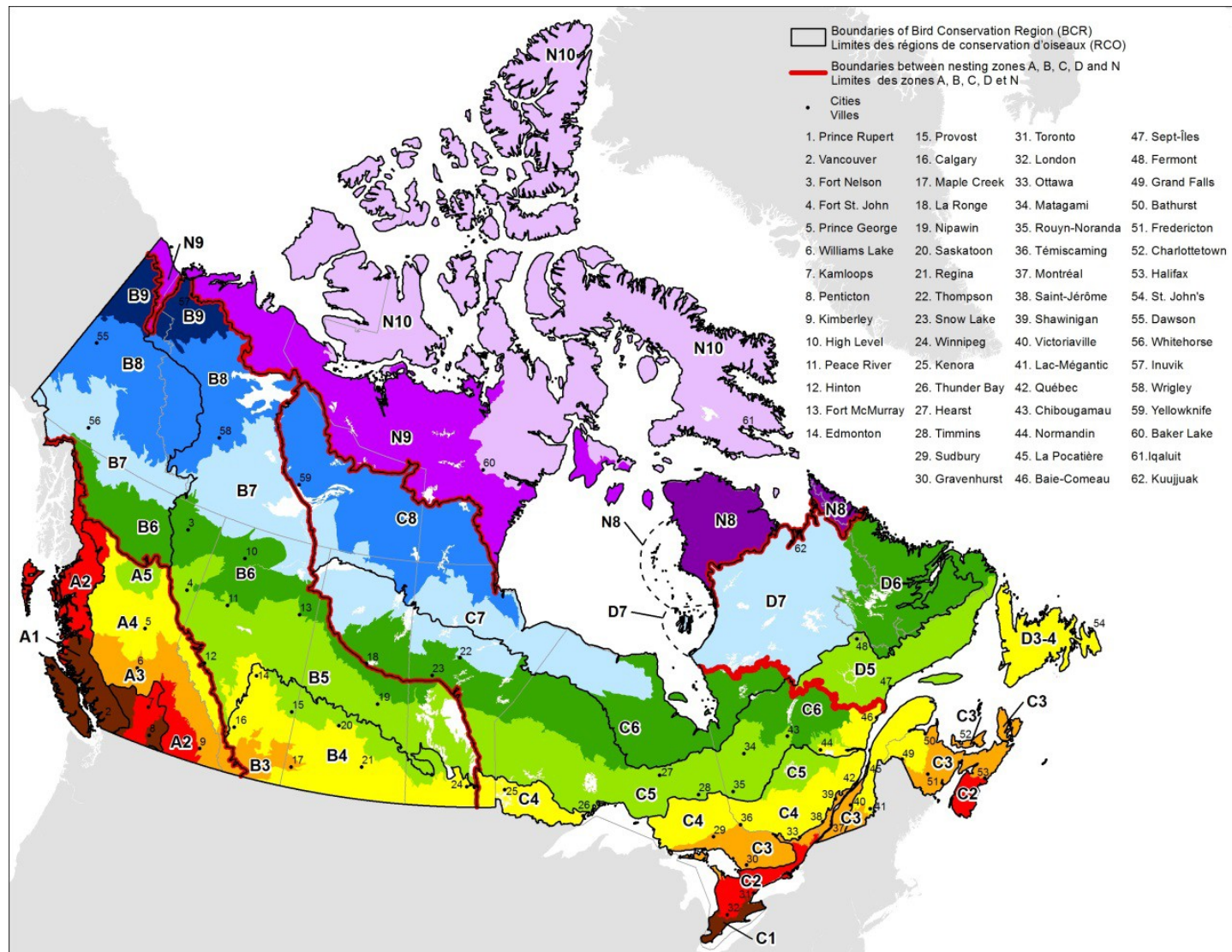


Figure 4.3. Map of the 27 nesting zones in Canada. Geographical proximity was used to assign a nesting zone to the ecodistricts lacking mean annual temperature values, or those that were not considered when establishing the nesting zones.

Table 4.3. Regional nesting periods of migratory birds estimated in third-of-month divisions for each nesting zone in Canada (early: 1st to 10th day of the month; mid: 11th to 20th day of the month; and late: 21st day to the end of the month)

Nesting zone	Regional nesting period
A1	Late March to mid-August
A2	Early April to mid-August
A3	Mid-April to mid-August
A4 and A5	Late April to mid-August
B3 and B4	Mid-April to late August
B5	Mid-April to late August
B6	Late April to mid-August
B7 and B8	Early May to late August
B9	Mid-May to mid-August
C1	Late March to late August
C2	Early April to late August
C3 and C4	Mid-April to late August
C5	Late April to late August
C6	Late April to mid-August
C7 and C8	Early May to mid-August
D3-4	Mid-April to mid-August
D5	Late April to mid-August
D6 and D7	Early May to mid-August
N8 and N9	Mid-May to mid-August
N10	Late May to mid-August

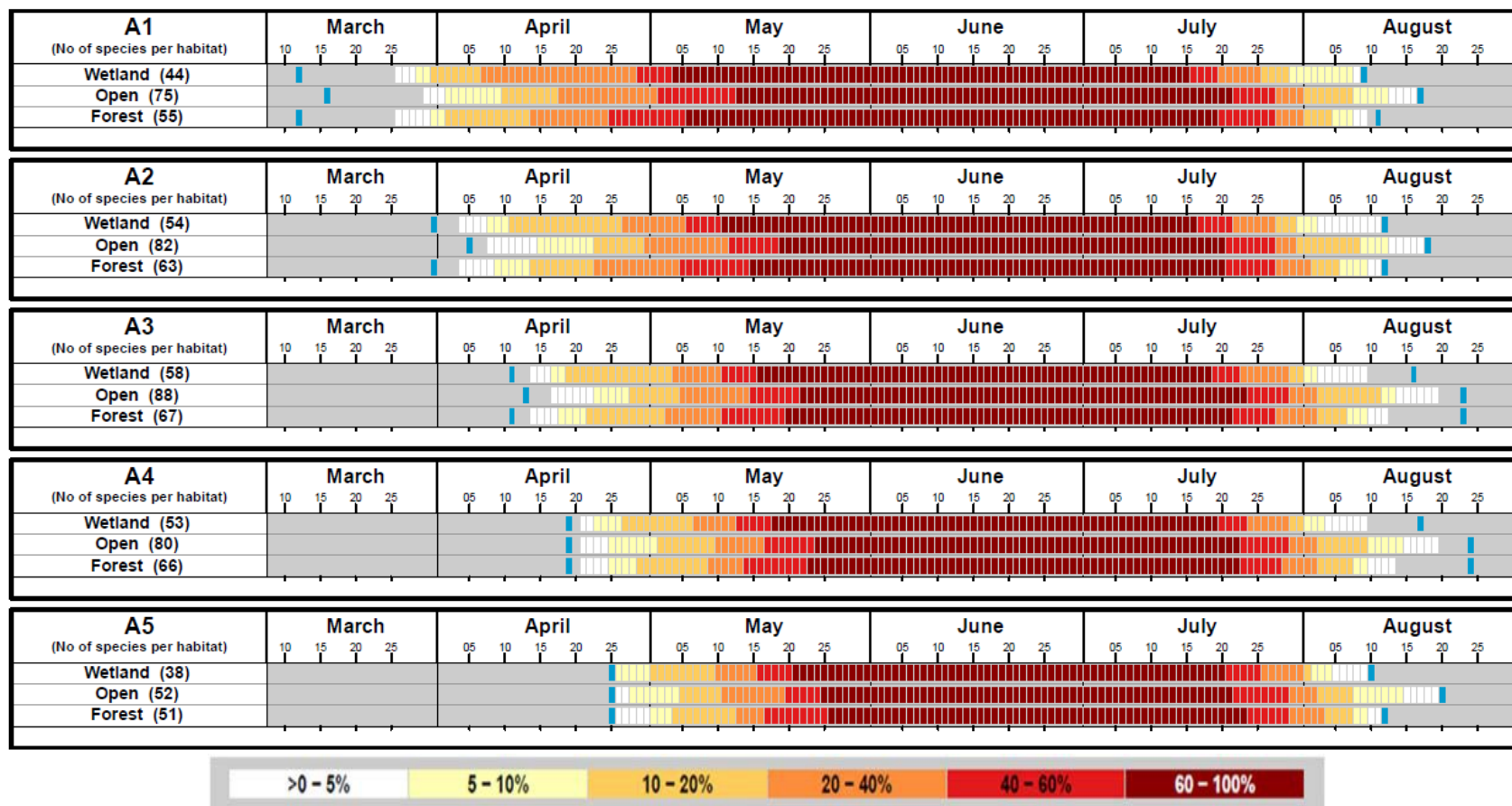


Figure 4.4. Regional nesting calendars for nesting areas in coarse zone "A", indicating the percentage of migratory bird species actively nesting. Blue milestones show the predicted extreme dates for some atypical parts of the nesting area where nests may be active earlier or later.

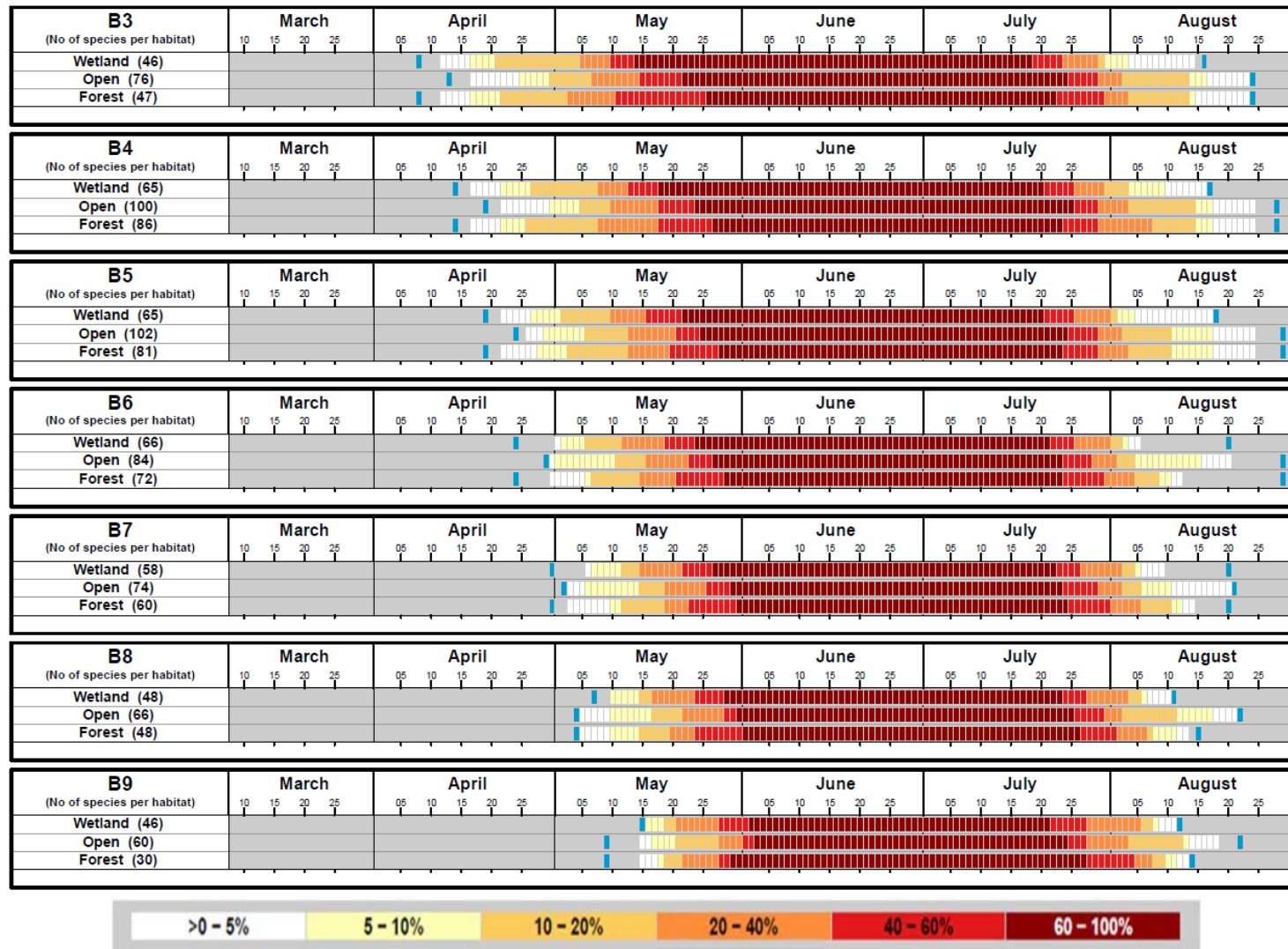


Figure 4.5. Regional nesting calendars for nesting areas in coarse zone "B", indicating the percentage of migratory bird species actively nesting. Blue milestones show the predicted extreme dates for some atypical parts of the nesting area where nests may be active earlier or later.

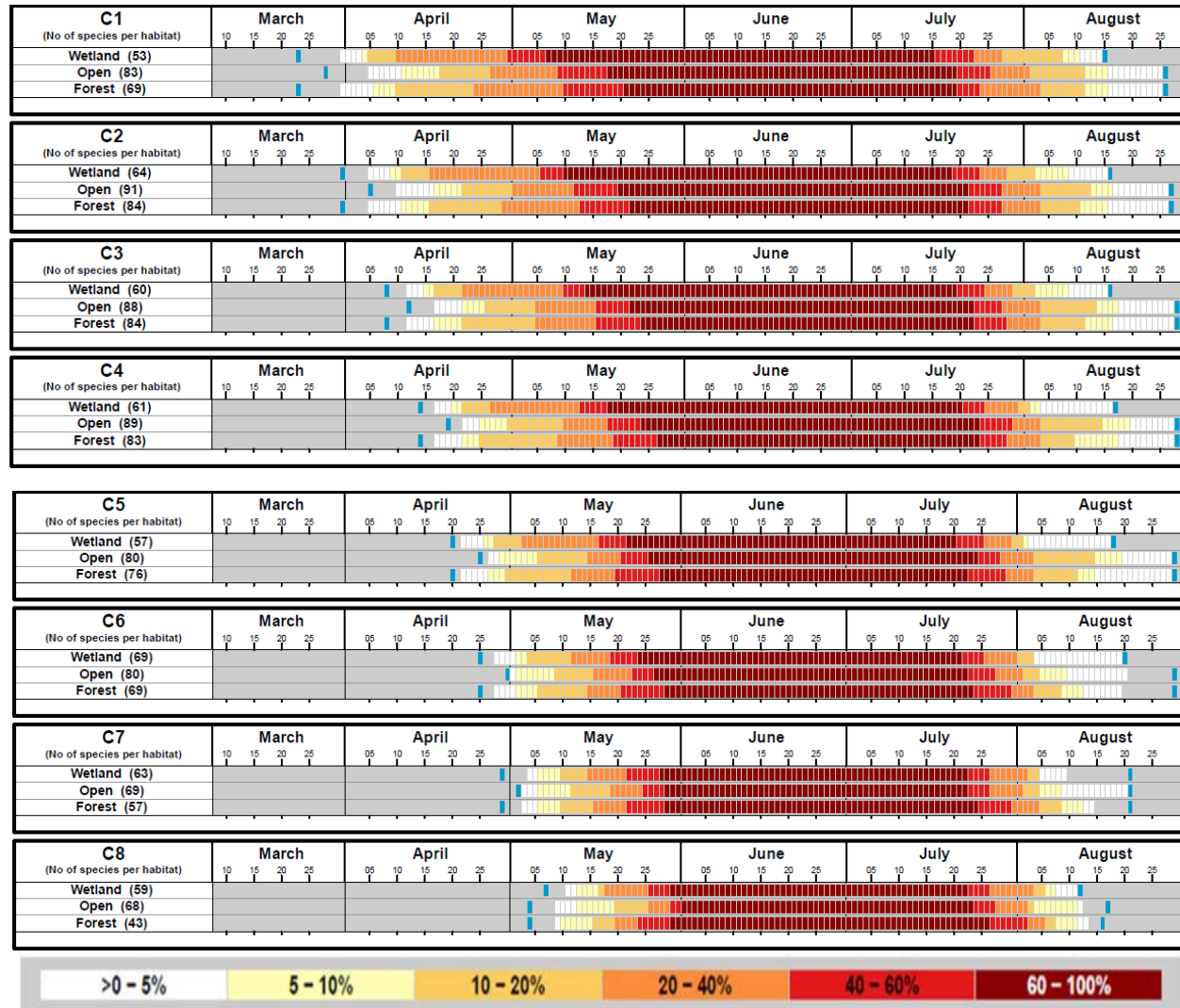


Figure 4.6. Regional nesting calendars for nesting areas in coarse zone "C", indicating the percentage of migratory bird species actively nesting. Blue milestones show the predicted extreme dates for some atypical parts of the nesting area where nests may be active earlier or later.

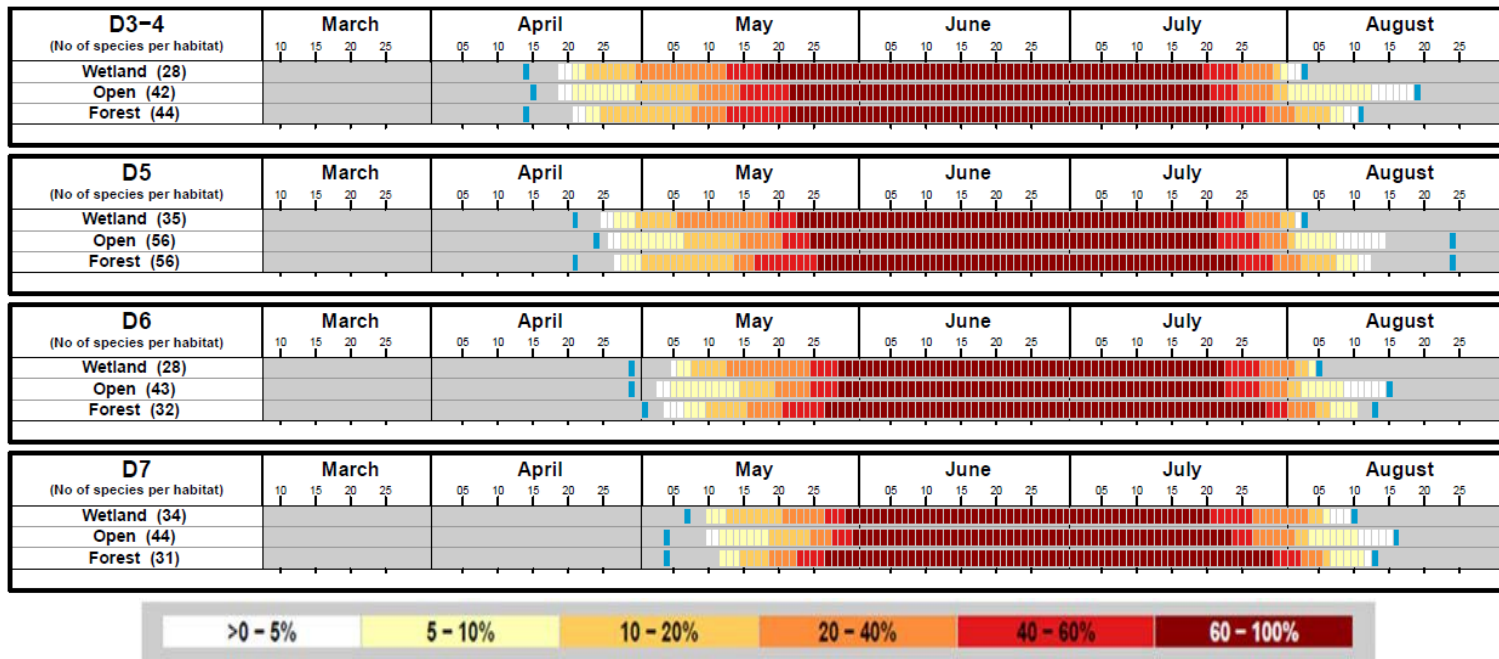


Figure 4.7. Regional nesting calendars for nesting areas in coarse zone "D", indicating the percentage of migratory bird species actively nesting. Blue milestones show the predicted extreme dates for some atypical parts of the nesting area where nests may be active earlier or later.

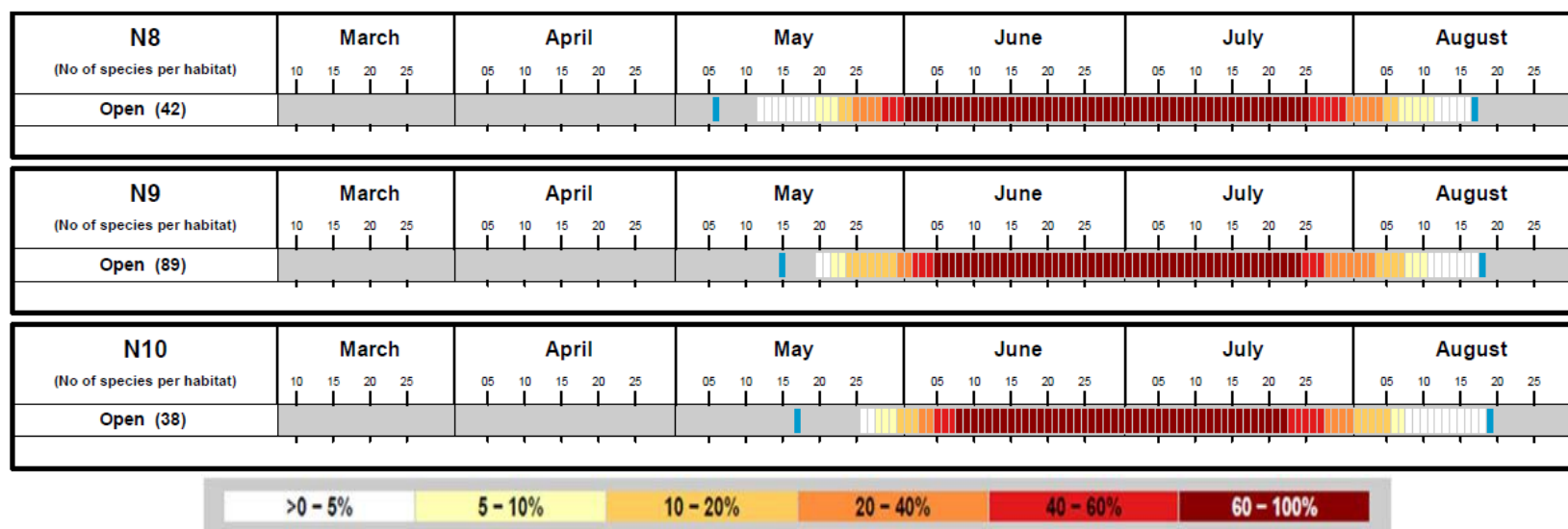


Figure 4.8. Regional nesting calendars for nesting areas in coarse zone "N", indicating the percentage of migratory bird species actively nesting. Blue milestones show the predicted extreme dates for some atypical parts of the nesting area where nests may be active earlier or later.

Accuracy of migratory bird nesting calendars

The aim of calculating regional nesting calendars was to provide an estimate, for extensive and relatively homogeneous zones, of the period when the majority of migratory birds were nesting. For this, the nesting phenology was used, rather than establishing record dates for the earliest and latest active nests.

Since regional calendars represent the median nesting period of ecodistricts within the nesting zones, the start and the end of the nesting period in any given ecodistrict may be slightly earlier and/or later than that provided by the calendars. Such discrepancies are shown on the nesting calendars (Figures 4.4 to 4.8) by the gap, mostly in the spring, between the extreme dates predicted for some atypical parts of the nesting zone (blue vertical bars) and the general nesting periods. On average, the time difference was small: 4.0 days (SD = 2.8 days) at the beginning and 2.6 days (SD = 4.2 days) at the end of the nesting period. However, for southern British Columbia (nesting zone A1), the earliest nesting dates in the spring were 13 to 14 days ahead of the general nesting periods. Such differences for the southern part of this province are due to the variety of micro-climatic conditions, within this nesting zone. This translates to birds nesting earlier in the coastal area than in the interior, with some species, such as the Song Sparrow, Great Blue Heron and Mallard, starting in February, and the Canada Goose, Common Merganser, Killdeer and Bushtit, in early March (BC Atlas, 2015). The same is also true at the end of the nesting period, with some species, such as swallows, wrens, chickadees, and the Bushtit, Swainson's Thrush and Dark-eyed Junco, still nesting in September (BC Atlas, 2015).

In the context of managing and preserving migratory birds, the nesting calendars provide global estimates of when most migratory bird species are likely to nest and how much the nesting activity varies during that period. When assessing the probability of active nests for a particular area, it is important to keep the following considerations in mind:

- **Consideration 1: Definition of the active period.** Regional nesting calendars were built from backcalculated nest observations, which estimated the period during which nests were considered active. However, the nesting chronology of birds involves several successive stages, including breeding site selection, mate choice, nest construction, laying and incubation, and raising of chicks in the nest and after

they have left. In the regional nesting calendars, the estimated nesting periods begins with the laying of the first egg and ends with the departure of the last chick from the nest. Thus, the earliest estimated dates do not take into account the period of nest construction prior to laying, and the latest estimated dates do not take into account the period with dependent young that have left the nest.

- **Consideration 2: Number of species vs. number of nests.** The intensity of nesting in the regional calendars is based on the number of species estimated to nest at any given time, not the number of individuals nesting. Therefore, periods with fewer nesting species may still have a high number of individuals nesting. For example, large numbers of Canada Geese, Mallards and Pintails nest in the Prairies (nesting zones B3 and B4; Figure 4.5) in April, but the nesting intensity is lower than in mid-summer (P. Grégoire, pers. comm.).
- **Consideration 3: Gradual changes in nesting periods.** Changes in the nesting period between adjacent nesting zones occur along a gradient. Therefore, to determine when migratory birds are most likely to be nesting near the boundary of a given zone, it is advisable to also consider the nesting period in adjacent zones.
- **Consideration 4: Nesting period of non-federally protected species.** The objective of calculating regional nesting calendars was to provide a regional estimate of the general nesting period for the majority of federally protected bird species (i.e., 83% of species nesting in Canada). Although the resulting regional calendars may encompass periods when non-federally protected species are nesting (e.g., corvids, owls, hawks, icterids, galliformes, cormorants and the kingfisher), they should not be relied on to portray their general nesting periods, as parts of the nesting period of some of these species may fall outside the dates given by the calendars provided in this report.
- **Consideration 5: Species that nest outside the predicted nesting periods.** The general nesting period may not be accurate for those species that, if conditions are appropriate, can breed at any time of the year such as crossbills; and species that may nest late in the season, such as waxwings, and the Pine Siskin and American Goldfinch (see Panel 4 of Part 2 – *Species Accounts*). Furthermore, it was not possible to establish the nesting phenology for 97 migratory birds due to a lack of adequate records or unsatisfactory models. Thus, although regional calendars may include periods when species not considered are nesting, they may be inaccurate for those species, in particular seabirds

(see Section 2.5 and Table 2.3). For example, the nesting periods may not be accurate for the Common Murre that may nest until the end of September, or the Leach's Storm-Petrel, Fork-tailed Storm-Petrel and Northern Gannet, which may still be nesting in October (Ainley *et al.*, 2002; Mowbray, 2002; Dee Boersma and Silva, 2001; Huntington *et al.*, 1996).

- **Consideration 6: General accuracy of predictions.** In general, the uncertainty surrounding the estimated nesting dates varied by a period of 10 days, or perhaps more in certain cases, due to the natural variability in the timing of nesting events between regions, individuals and years, and due to the sampling and the constraints associated with the methods used (see Chapters 2 and 3). Furthermore, it is possible that birds in a given location could have different start dates and/or nesting durations than those estimated for the nesting zone. This may be due to micro-climatic conditions in specific areas (e.g., high elevation or coastal sites, notably in British Columbia), as well as inter-annual variation due to factors such as an early spring or a cold, wet summer. As a result, migratory birds may be nesting before and/or after nesting periods presented in the regional nesting calendars. The probability of the presence of active nests outside these nesting periods is much lower, but not null.
- **Consideration 7: Accuracy of the nesting prediction in British Columbia.** Compared to other regions, the estimation of the nesting periods for British Columbia was negatively affected by the lack of precision of nest locations (reported using the centroid of the relevant breeding bird atlas square), a lack of non-landbirds nest records, and the effect of altitudinal variation (non-perceptible with the MAT values used), where the nesting period within the same ecodistrict can start later at higher elevations and earlier in lower lying valleys.

GENERAL CONCLUSION

To our knowledge, this is the first attempt to produce a nationally consistent and unified description of bird nesting phenology across the different provinces and territories of Canada. This technical report, which proposes a coherent and standardized way to infer and describe nesting phenology, makes use of the hundreds of thousands of nest observations contained in the Project NestWatch database maintained by Bird Studies Canada. The first part of this report details the methods used to estimate nest chronology and model nesting phenology, and the second part provides a nesting summary for 376 wild bird species breeding in Canada. The latter also presents the overall results, including species-specific predictions of the nesting period of 311 species, which represents 71% of bird species breeding in Canada.

Processing the entire Project NestWatch database required the development of a sound backcalculation procedure to make the most of the observations in each of the nest records. Technically, the challenge was to develop a complex set of algorithms to estimate the most likely nest chronology for each nest record. The coding of these algorithms into a package of R-language functions, named *rNest*, paved the way for the automated processing of nearly half a million nest visits, and the calculation not only of nesting periods, but also of the nesting intensity of hundreds of species. This package, which was designed for general use, is now in the public domain (Rousseu and Drolet, 2017a), and will undoubtedly save time for future users.

The estimation of bird nesting phenology required the development of a multifaceted methodological approach to account for several potential sources of bias, including the uneven distribution of nest records both geographically and between species. One of the significant contributions resulting from this study is the proposed nesting period estimates for northern Canada, for which nest observation data were scarce. Although the analyses probably suffered from this lack of information, the use of a standardized method applied to all regions of Canada allowed nesting phenology predictions to be provided for northern regions. It should be noted that these predictions benefited greatly from data compiled for Nunavut by Coulton and Robertson (2009), and data from the Northwest Territories /Nunavut Bird Checklist Survey (EC, 2014). As more data become available, either through Project NestWatch or other sources, this will open up the possibility of new analyse to improve the models and predictions.

Another important contribution of this study is that it provides estimates of nesting periods for species for which there are few nest records, either generally or locally, and an assessment of the uncertainty of these estimates. To give an idea of the level of accuracy obtained using the modelling process, each prediction curve is accompanied by confidence intervals. Furthermore, uncertainty mapping is provided for most species, allowing visualization of the nesting area of a given species divided into two predictions zones with different levels of confidence.

This study also allowed an in-depth analysis of the relevance of using the backcalculation procedure when establishing nesting chronologies. Although it is difficult to eliminate methodological biases, the simulations that were run show, in particular, that it is more advantageous to use backcalculated dates than the raw observation dates, and that the biases can be attenuated by appropriate uncertainty-based weighting factors. However, it should be borne in mind that for the nesting period estimates presented in this report, the effect of these biases was generally low, or negligible, compared to uncertainty levels, even for a species with a long nesting period.

Finally, estimation of nest chronology and modelling of nesting phenology generated a considerable amount of information about each species, and different means of presenting this were developed. The first of these takes the form of regional nesting calendars for federally protected species, which give a condensed picture, for each of the nesting zones, of the evolution of the intensity in terms of the number of nesting species across Canada. These results are presented in Chapter 4 and are also publicly available on the Environment and Climate Change Canada website (ECCC, 2017a). The second provides species-specific nest summaries to facilitate access to the information used in the analyses, as well as the results and the predictive models concerning the nest phenology. Although very much a summary, these reports should be highly useful to those who require species-specific information for the management and conservation of breeding birds. These results are presented in Part 2 of this report and general nesting periods for each modelled species are also publicly available through the *Status of Bird in Canada* website (ECCC, 2017b). The third tool developed was an interactive on-line resource that allows the creation of customized nesting calendars based on the species and regions of interest. This tool, the “Nesting Calendar Query Tool”, is available through the Project NestWatch section of the Bird Studies Canada website (Rousseu and Drolet, 2015). The

advantage of this tool is that it provides estimates of nesting periods for each species, *and* for each of the 1021 ecodistricts. The resulting nesting calendars are constructed using the main portion of the nesting season and can be sorted into different categories of interests (i.e., species, ecodistrict, bird conservation region, ecoregion, nesting zone, province or territory, federal protection, habitat, nest type and/or species group).

Although the results of this study propose more accurate and specific nesting period estimates than those previously available, this is the first attempt to model this on a Canada-wide scale and, like all models, it will need to be validated and refined. In spite of this, since the results of this study are methodologically and biologically sufficiently valid and respond to an immediate need by various stakeholders, who are challenged with the need to protect nests and eggs of wild birds breeding in Canada, it was considered appropriate that they be disseminated widely. In the future, several aspects of the analyses could be enhanced and it is hoped that the present study will lead to further development in this field and to new nest records being submitted to the Project NestWatch database. These records, whether contemporary or historical, are essential to better describe nesting phenology in certain regions or for certain species. Notable gaps in the data include a general lack of nesting records for Newfoundland and Labrador, and for northern Canada, together with a lack of data for non-landbird species in British Columbia, for waterfowl throughout Canada, and for uncommon, local, rare or inconspicuous species, and for breeding species new to Canada.

In conclusion, it is hoped that this study will stimulate a deeper understanding of bird nesting phenology in Canada, as did the colossal compilation that Peck and James produced for Ontario in 1983. However, as with the latter, this technical report largely presents the nesting phenology for the 20th century. In the context of climate change, it will be essential to periodically re-evaluate bird nesting phenology in Canada to take in to account the effect of new environmental conditions and to document possible changes to the nesting periods. However, when the current analyses were conducted on the available data, no such changes were perceptible.

PART 2: SPECIES ACCOUNTS

INTRODUCTION

This part of the technical report contains an individual account for 376 of the 439 bird species considered to nest in Canada (EC, 2015b). These accounts are based on nest records from the Project NestWatch databases (BSC, 2013), data compiled for Nunavut by Coulton and Robertson (2009), and data from the Northwest Territories/Nunavut Bird Checklist Survey (EC, 2014). For 335 of the species, the accounts contain all the information that was considered for, and generated by, the analyses, including the values and the information used to estimate the nest chronology through backcalculation, the active nesting periods obtained from nest observations (see Part 1, Chapter 1 for a detailed explanation), and the results and models predicting nesting phenology across the breeding range of the species (see Part 1, Chapters 2 and 3 for details).

The species accounts also contain the location of the nest records used, and the proportion of active nests from backcalculated nest observations for species that, due to lack of sufficient data, were not considered in the analyses ($n = 41$ species). Although only summary information, this nevertheless shows the details that can be extracted from the Project NestWatch database for these species. One of the main reasons for including this information was to help identify existing gaps, with the hope of attracting additional contributions of new or historical data to the Project NestWatch database (see Part 1, Section 2.3 for the list of species, and Section 2.5 - *Future directions for improvements*). Please note, however, that the species known to nest in Canada, but for which there were no nest records in the Project NestWatch database, are not included in the species accounts ($n = 63$ species, see list below).

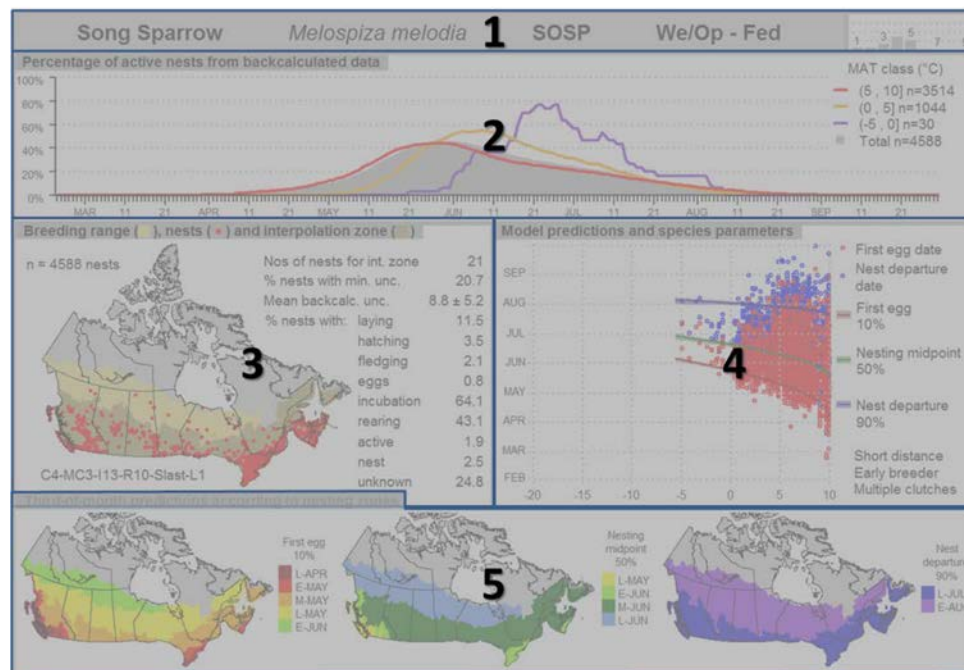
For the vast majority of species, the name used is that found on the list provided in 2015 by Environment and Climate Change Canada (ECCC, 2015b). However, in the case of three species that have recently been divided, the old name was retained. This was due to overlap in the breeding ranges of the newly recognised species, which made it impossible to correctly classify the nest records according to species. The species in question were the Winter Wren (*Troglodytes troglodytes*), now the Winter Wren (*T. hiemalis*) and the Pacific Wren (*T. pacificus*); the Western Flycatcher (*Empidonax occidentalis*), now the Cordilleran Flycatcher (*E. occidentalis*) and the Pacific-slope Flycatcher (*E. difficilis*); and the Canada Goose (*Branta*

canadensis), now the Canada Goose (*B. canadensis*) and the Cackling Goose (*B. hutchinsii*).

Finally, as mentioned previously, predictions for each species *and* ecodistrict are available on the Bird Studies Canada website under the "Nesting Calendar Query Tool" of the Project NestWatch section (Rousseu and Drolet, 2015). This tool also allows the creation of customized nesting calendars for a selection of species and regions of interest (see Part 1, Figure 2.6).

DETAILED DESCRIPTION OF THE SPECIES ACCOUNTS

The information is presented in five panels as shown in the example for the Song Sparrow below.



Example of a species account: the Song Sparrow. The numbers indicate the panel in which the information is presented. Abbreviations are explained in the main text and a summary list is provided at the end of this section.

Panel 1

This panel, which is located at the top of each species account, provides the common name, the scientific name and the American Ornithologists Society's four-letter code for the species (EC, 2015b). To the right of these is the code for the habitat type(s) in which the species is known to nests: **Fo** (forested), **Op** (open) and/or **We** (wetland). Open habitat includes environments such as urban landscapes, farmland, clearings, upland meadows, coastal areas, cliffs and tundra. The

classification of species by habitat was based on Godfrey (1986), Ehrlich *et al.* (1988) and the *Birds of North America Online* (2015), but is still somewhat subjective and debatable, especially considering the variety of nesting habitats used by some species and the uncertain distinction between some types of open and wetland habitat, and between some types of wetland and forest habitat. These habitat types were used for building the regional nesting calendars for the federally protected species (see Part 1, Chapter 4 for details). The code given after the habitat indicates whether the species is federally protected under the *Migratory Bird Convention Act, 1994* or not: **Fed** (federally protected species) or **NFed** (non-federally protected species; EC, 2015b). The bar chart on the far right of the panel shows the proportion of nest visits during which a given number of eggs were observed. The three horizontal broken lines show the 25%, 50% and 75% lines, and the numbers show the number of eggs associated with each bar. The values shown were restricted to those visits where at least one egg was counted, and to nests that were used in the modelling process. These data are provided to justify the clutch size value used in the backcalculations and to show potential clutch size values found in Canada. It should be noted that these values do not necessarily indicate clutch size during incubation, as all visits with eggs were included (which could have comprised visits made during the laying period), but they can be used to estimate clutch size. In most cases, the clutch size used to estimate the nest chronologies was the modal number of eggs but, when the distribution of clutch sizes had no clear modal value, a number was subjectively chosen based on the most likely value. The estimated and minimal clutch size values retained are shown in panel 3.

Panel 2

This panel, which is located directly under panel 1, shows the daily proportion of active nests across the nesting season. It is entirely based on backcalculated nesting events using the nest observations available. For most species, this figure only contains information from nests included in the modelling process; however, for non-modelled species, all backcalculated nest data are shown. A nest is considered active from the day when the first egg is laid, to the day when the last young leaves the nest. Therefore, the earliest estimated dates do not take into account the period of nest construction prior to laying, and the latest estimated dates do not take into account the period when young are dependent on their parents outside the nest. The proportion of active nests is presented in two ways: the first provides the proportion of active

nests for all nests used, without considering temperature (gray bars); and the second provides the proportion of active nests within mean annual temperature classes (**MAT**, °C, coloured curves). The data are divided into four MAT classes to show the variation in the timing of nesting across the breeding range of the species. The legend on the right-hand side describes the MAT classes, with the number of nests contained in each class (**n**). The symbol "]" indicates inclusion of the value, while the symbol "(" indicates exclusion of the value. Only the proportions of active nests for temperature classes for which there were at least 15 nests are shown.

Panel 3

This panel, which is located on the middle left of the species account, shows a map of Canada (in light gray) with the merged area of the ecodistricts (in light and/or dark brown) *considered to overlap the breeding range* of the species, as established by BirdLife International (Ridgely *et al.*, 2003), along with the number (**n**) and location of nest records (red dots) that were used in the modelling process. To show the extent of ecodistricts in which a species was considered to be present, the margin of the area of the merged ecodistricts was used instead of the boundaries of the true breeding range. Consequently, it is important to keep in mind that these maps ***do not represent*** the exact extent of the breeding range. For some species, regions that are not part of the breeding range are included because parts of some ecodistricts are located outside the breeding range. In other cases, gaps appear on the map of some species because large ecodistricts that extend outside the breeding range enclose smaller ecodistricts that do not overlap with the species breeding range. Finally, in some cases, nest records may be located outside the breeding range because distribution maps for some species (e.g., Barrow's Goldeneye) were not up to date. For most species, the map shows two shades of brown: the darker indicates the interpolation area, where predictions are associated with a higher degree of certainty, and the lighter show the extrapolation area, where predictions should be used with greater caution (see Part 1, Section 3.3 for more details).

A range of additional information is given in this panel. The coded information below the map provides the name of the nesting parameters and the values used for the backcalculations: **C** (estimated clutch size); **MC** (minimum clutch size used to consider a nest still at the "laying" stage); **I** (length of incubation period in days); **R** (length of rearing period in days); **S** (the onset of incubation in terms of either egg number (e.g., **S1** after the first egg, **S2** after the second egg,

etc.), or **Sblast** considered to be with the penultimate egg laid or **Slast** considered to be with the last egg laid); and **L** (laying interval in days). To the right of the map, there is further information. The first three lines refer to the values that define the interpolation area (see Part 1, Chapter 3 for details): the number (**Nbr**) of nests required to reach an expected standard error of ± 10 days, which was used to defined the interpolation zone (**int. zone**); the percentage (%) of nests backcalculated with the greatest certainty (**min. unc.**), which largely corresponds to the total percentage of nests with observations during the "laying", "hatching" or "fledging" stages; and the mean backcalculation uncertainty in days (\pm the standard deviation). The following nine lines describe the percentage of nests with at least one visit classified in the following nesting stage codes, ordered from minimum to maximum uncertainty for backcalculated dates: "laying", "hatching", "fledging", "eggs", "incubation", "rearing", "active", "nest" or "unknown" (see Part 1, Chapter 1 for details, in particular Table 1.2).

Panel 4

This panel, which is located on the middle right of the species account, shows the predictions derived from the modelling process to infer the nesting phenology across the mean annual temperature (MAT) range experienced by a given species within its normal breeding distribution. The red circles are the backcalculated first egg dates and the red curve is the predicted first egg date for the MAT range when 10% of first eggs will have been laid. The blue circles are the backcalculated departure dates and the blue curve shows the predicted dates when 90% of nests will have been vacated by young. The green curve shows the predicted nesting midpoint dates, at which 50% of nests will have reached the middle of their active period. The shaded colour around each prediction curve shows the 95% confidence interval. This information provides an assessment of the uncertainty associated with the predictions that is complementary to the uncertainty shown by the interpolation/extrapolation zones (see Part 1, Section 2.3 for details). Larger confidence intervals are associated with greater uncertainty in predictions. The models comprise five explanatory variables: the MAT, the species, the migratory strategy (**resident**, **short**, **mid-** or **long distance** migrant), the tendency to breed early (**early** or **late breeder**) and the capacity to lay multiple clutches (**single clutch** or **multiple clutches**) (see Part 1, Chapter 2 for definitions). The values of the latter three variables are provided at the bottom right of the panel. For 41 species, no prediction curves are shown because there were an insufficient number

of nest records to allow modelling. In these cases, only the estimated nesting dates (red and blue circles) are presented. Finally, in the case of the species for which the models were rejected due to a poor fit with the available data ($n = 24$), the predictions curves are masked with a transparent gray layer (see Part 1, Section 2.4 for details), and the reason for rejection is shown on the graph.

Panel 5

This panel, which is located at the bottom of each species account, shows the predictions of the three models highlighted in Panel 4 (**first egg 10%, nesting midpoint 50% and nest departure 90%**) in third-of-month divisions for all nesting zones overlapping the breeding range of the species. Although a single predicted date could have been given for each model and for each nesting ecodistrict, it was felt more appropriate, given the possible uncertainty associated with the data and the modelling process, to provide the predictions in third-of-month divisions (see below) and to present the predictions at the scale of nesting zones rather than ecodistricts.

Furthermore, it allows the user to gain a general idea of the nesting period in different regions, without relying on potentially unrealistically precise predictions (see Part 1, Chapter 3 for details about biases and uncertainties related to predictions, and Part 1, Chapter 4 for details about the nesting zones).

The prediction in third-of-month divisions was established by first determining the predicted date for a given model for each ecodistrict. After this, the median of the predicted dates for the various ecodistricts, weighted based on the area of each ecodistrict within the nesting zone of the species, was calculated using the nesting zones constructed for the regional nesting calendars (see Part 1, Chapter 4 for details). The median date was then attributed to its appropriate third-of-month division: **E**- (early, 1st to 10th day of the month), **M**- (mid, 11th to 20th day of the month) and **L**- (late, 21st day of the month to end of month). High contrast colours have been used in the maps to allow better discrimination between divisions, and the range of colours was determined by the extent of the dates predicted for the species. Once again, please note that the margin of the third-of-month prediction area follows the limits of the area of the merged ecodistricts, in which the species occurs, rather than the true limits of the breeding range established from the BirdLife International data (Ridgely *et al.*, 2003). Thus, the boundaries showed may extend outside the true limits of the breeding range (see Panel 3 description above for more details). For a species with a small breeding range, the prediction areas shown on the map might have unnecessary

ragged contours. This is a consequence of using precise ecodistrict limits to build the prediction area. Finally, the third-of-month prediction areas shown in Panel 5 are associated with broad geographical areas across the range of the species and occur along a gradient. Therefore, if a given place of interest is located near the boundary between two third-of-month divisions, it is advisable to consider both periods when determining when the species is most likely to be nesting (see the cautionary note at the beginning of the report and Part 1, Section 4.3, Considerations 1, 3 and 6).



(Photo: Stilt Sandpiper on nest; F. Rousseu)

List of abbreviations in the species accounts

C:	Estimated clutch size
E-:	Early (1 st to 10 th of the month)
Early breeder:	If 2% of first eggs were laid on or before April 20 th anywhere in Canada
Fed:	Federally protected species
Fo:	Forest nesting species
I:	Length of incubation period in days
L-:	Late (21 st to end of the month)
L1, L2, etc.:	Laying interval in days
Late breeder:	If 2% of first eggs were laid after April 20 th anywhere in Canada
M-:	Mid- (11 th to 20 th day of the month)
MAT:	Mean annual temperature (°C)
MC:	Minimum clutch size used to consider a nest still at "laying" stage
n:	Number of nest records
NFed:	Non-federally protected species
Op:	Open area nesting species (including urban landscapes, farmland, clearings, upland meadows, coastal areas, cliffs and tundra)
R:	Length of rearing period in nest in days
S1, S2, etc.:	Onset of incubation considered to be with 1 st egg laid, 2 nd egg laid, etc.
Sblast:	Onset of incubation considered to be with the penultimate egg laid.
Slast:	Onset of incubation considered to be with the last egg laid.
unc.:	Uncertainty
We:	Wetland nesting species

Phylogenetical list of species known to nest in Canada, which are not included in the species accounts due to a lack of nest records or because of recent taxonomic changes.

English Name	French Name	Scientific Name
Chukar	Perdrix choukar	<i>Alectoris chukar</i>
Sooty Grouse	Tétras fuligineux	<i>Dendragapus fuliginosus</i>
Clark's Grebe	Grèbe à face blanche	<i>Aechmophorus clarkii</i>
Northern Fulmar	Fulmar boréal	<i>Fulmarus glacialis</i>
Manx Shearwater	Puffin des Anglais	<i>Puffinus puffinus</i>
Fork-tailed Storm-Petrel	Océanite à queue fourchue	<i>Oceanodroma furcata</i>
Northern Gannet	Fou de Bassan	<i>Morus bassanus</i>
Brandt's Cormorant	Cormoran de Brandt	<i>Phalacrocorax penicillatus</i>
Great Cormorant	Grand Cormoran	<i>Phalacrocorax carbo</i>
Pelagic Cormorant	Cormoran pélagique	<i>Phalacrocorax pelagicus</i>
Snowy Egret	Aigrette neigeuse	<i>Egretta thula</i>
White-faced Ibis	Ibis à face blanche	<i>Plegadis chihi</i>
Mississippi Kite	Milan du Mississippi	<i>Ictinia mississippiensis</i>
Whooping Crane	Grue blanche	<i>Grus americana</i>
American Oystercatcher	Huîtrier d'Amérique	<i>Haematopus palliatus</i>
Black Oystercatcher	Huîtrier de Bachman	<i>Haematopus bachmani</i>
Snowy Plover	Pluvier neigeux	<i>Charadrius nivosus</i>
Common Ringed Plover	Pluvier grand-gravelot	<i>Charadrius hiaticula</i>
Mountain Plover	Pluvier montagnard	<i>Charadrius montanus</i>
Eskimo Curlew	Courlis esquimau	<i>Numenius borealis</i>
Dovekie	Mergule nain	<i>Alle alle</i>
Common Murre	Guillemot marmette	<i>Uria aalge</i>
Razorbill	Petit Pingouin	<i>Alca torda</i>
Pigeon Guillemot	Guillemot colombin	<i>Cepphus columba</i>
Marbled Murrelet	Guillemot marbré	<i>Brachyramphus marmoratus</i>
Ancient Murrelet	Guillemot à cou blanc	<i>Synthliboramphus antiquus</i>
Cassin's Auklet	Starique de Cassin	<i>Ptychoramphus aleuticus</i>
Rhinoceros Auklet	Macareux rhinocéros	<i>Cerorhinca monocerata</i>
Atlantic Puffin	Macareux moine	<i>Fratercula arctica</i>
Horned Puffin	Macareux cornu	<i>Fratercula corniculata</i>
Tufted Puffin	Macareux huppé	<i>Fratercula cirrhata</i>
Black-legged Kittiwake	Mouette tridactyle	<i>Rissa tridactyla</i>
Ivory Gull	Mouette blanche	<i>Pagophila eburnea</i>
Ross's Gull	Mouette rosée	<i>Rhodostethia rosea</i>
Laughing Gull	Mouette atricille	<i>Leucophaeus atricilla</i>

Western Gull	Goéland d'Audubon	<i>Larus occidentalis</i>
Iceland Gull	Goéland arctique	<i>Larus glaucoides</i>
Glaucous-winged Gull	Goéland à ailes grises	<i>Larus glaucescens</i>
Roseate Tern	Sterne de Dougall	<i>Sterna dougallii</i>
Band-tailed Pigeon	Pigeon à queue barrée	<i>Patagioenas fasciata</i>
Eurasian Collared-Dove	Tourterelle turque	<i>Streptopelia decaocto</i>
Western Screech-Owl	Petit-duc des montagnes	<i>Megascops kennicottii</i>
Northern Pygmy-Owl	Chevêchette naine	<i>Glaucidium gnoma</i>
Spotted Owl	Chouette tachetée	<i>Strix occidentalis</i>
Common Poorwill	Engoulevent de Nuttall	<i>Phalaenoptilus nuttallii</i>
Black Swift	Martinet sombre	<i>Cypseloides niger</i>
Vaux's Swift	Martinet de Vaux	<i>Chaetura vauxi</i>
White-throated Swift	Martinet à gorge blanche	<i>Aeronautes saxatalis</i>
Black-chinned Hummingbird	Colibri à gorge noire	<i>Archilochus alexandri</i>
Anna's Hummingbird	Colibri d'Anna	<i>Calypte anna</i>
Lewis's Woodpecker	Pic de Lewis	<i>Melanerpes lewis</i>
Williamson's Sapsucker	Pic de Williamson	<i>Sphyrapicus thyroideus</i>
Red-breasted Sapsucker	Pic à poitrine rouge	<i>Sphyrapicus ruber</i>
White-headed Woodpecker	Pic à tête blanche	<i>Picoides albolarvatus</i>
Cassin's Vireo	Viréo de Cassin	<i>Vireo cassinii</i>
Gray-headed Chickadee	Mésange lapone	<i>Poecile cinctus</i>
Kirtland's Warbler	Paruline de Kirtland	<i>Setophaga kirtlandii</i>

EXAMPLES OF HOW BEST TO DESCRIBE THE PREDICTIONS PROVIDED IN A SPECIES ACCOUNT

Example 1 – Description of a general nesting period with a small confidence interval

The general nesting period of the [*species name*], which covers the period from the laying of first eggs up until the moment when the young have naturally left the vicinity of the nest, may start anywhere between [*earliest first egg third-of-month division*] and [*latest first egg third-of-month division*], and may end anywhere between [*earliest nest departure third-of-month division*] and [*latest nest departure third-of-month division*], depending on latitude. In general, uncertainty surrounding the estimated nesting dates varies by a period of up to 10 days. Before and after these dates, the probability of an active nest occurring is lower, but not null (Rousseu and Drolet, 2017b). This nesting period was generated from predictive models based mainly on the mean annual temperature and mainly using nest records from Project NestWatch (BSC, 2013).

Example 2 – Description of a general nesting period for a region of interest

In [*region of interest*], the general nesting period of the [*species name*], which covers the period from the laying of first eggs up until the moment when the young have naturally left the vicinity of the nest, may start as early as [*earliest first egg third-of-month division for the area of interest*] and may extend up until [*latest nest departure third-of-month division for the area of interest*]. In general, uncertainty surrounding the estimated nesting dates varied by a period of up to 10 days. Before and after these dates, the probability of an active nest occurring is lower, but not null (Rousseu and Drolet, 2017b). This nesting period was generated from predictive models based mainly on the mean annual temperature and mainly using nest records from Project NestWatch (BSC, 2013).

Example 3 – Description of a general nesting period with a large confidence interval

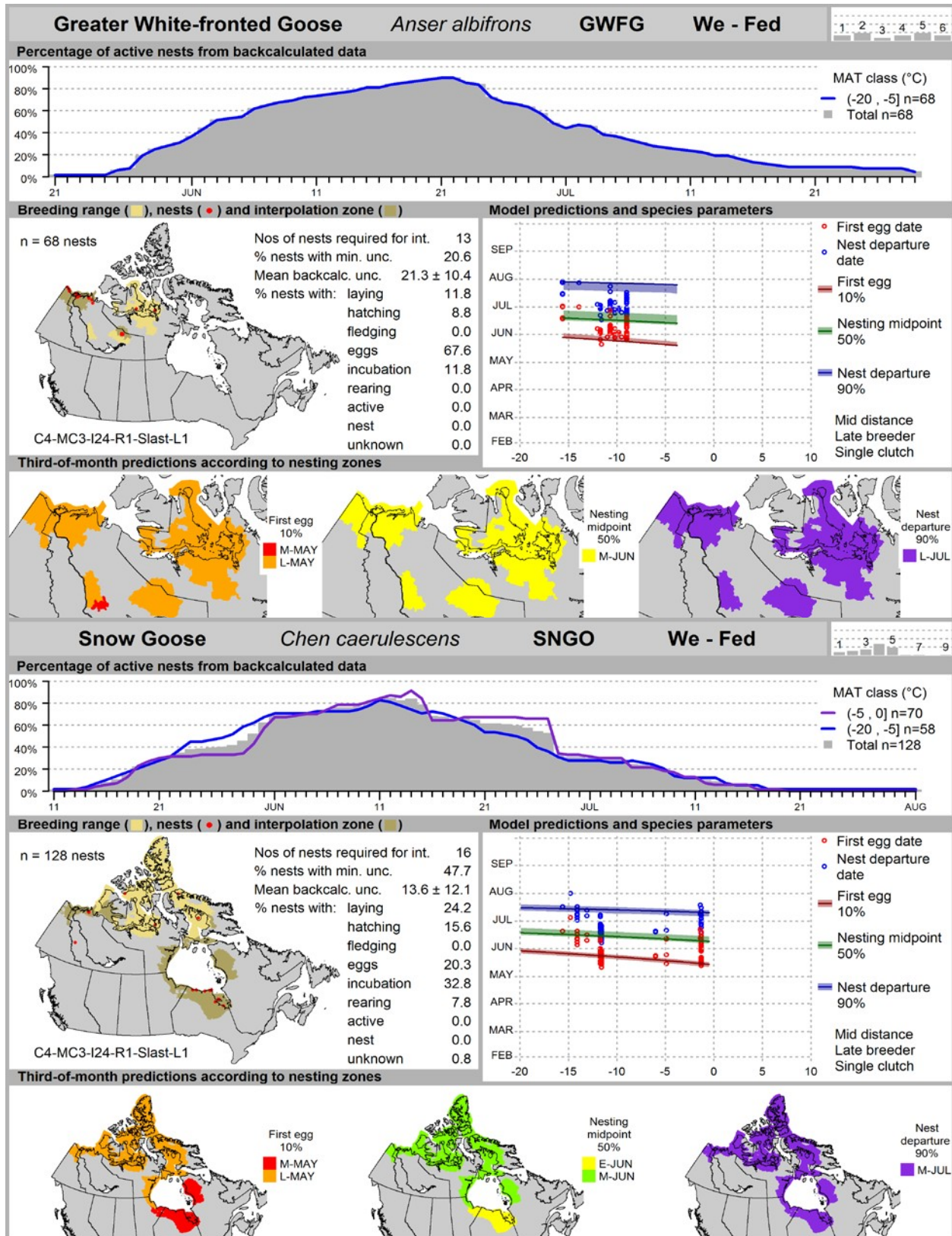
In [*region of interest*], the general nesting period of the [*species name*], which covers the period from the laying of first eggs up until the moment when the young have naturally left the vicinity of the nest, may start anywhere between [*earliest first egg third-of-month division considering*

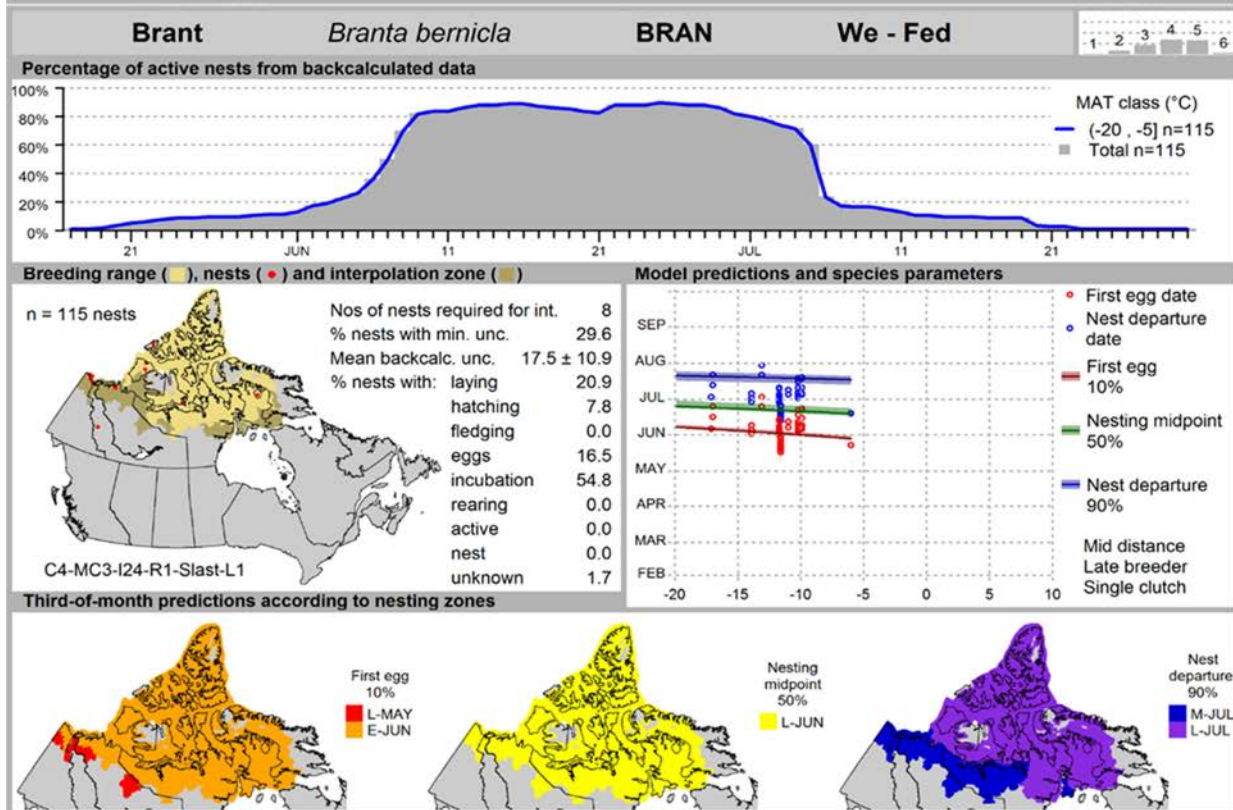
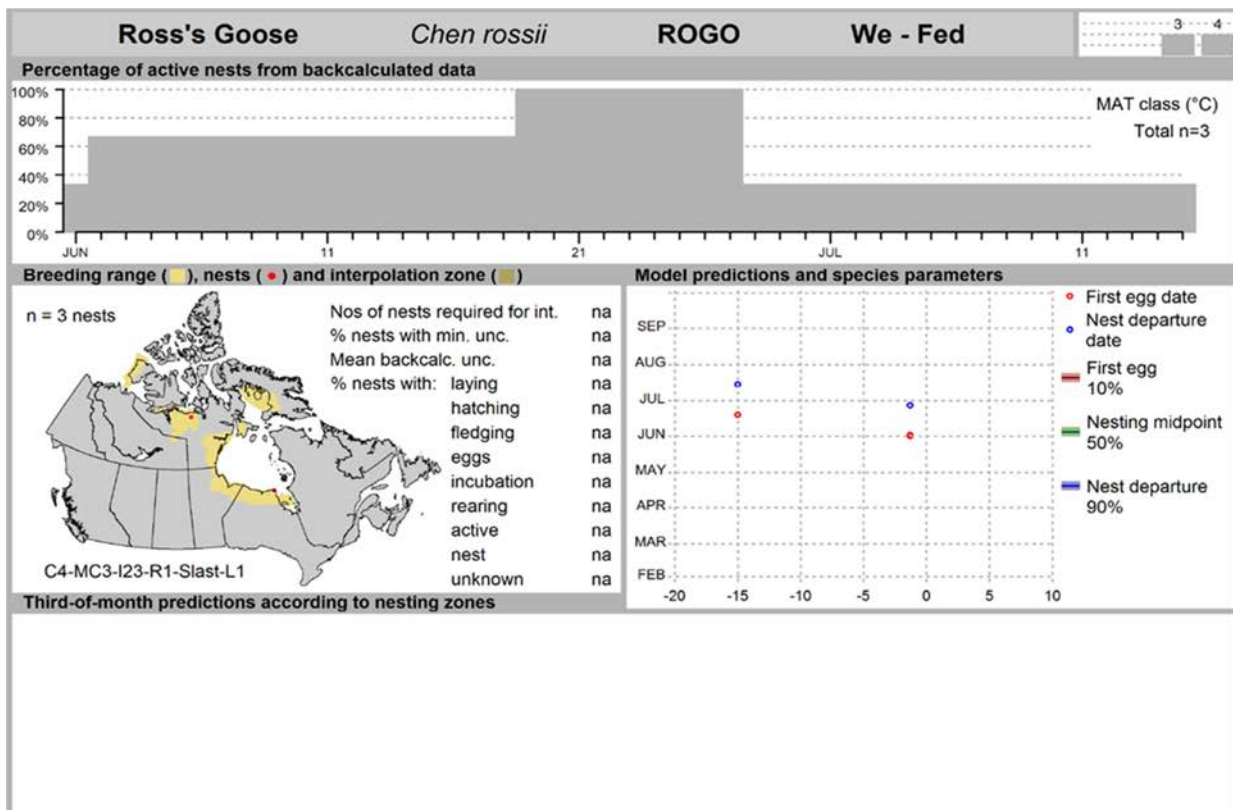
the lower limit of the confidence interval for the area of interest] and *[latest first egg third-of-month division considering the upper limit of the confidence interval for the area of interest]*, and may extend up until anywhere between *[earliest nest departure third-of-month division considering the lower limit of the confidence interval for the area of interest]* and *[latest nest departure third-of-month division considering the upper limit of the confidence interval for the area of interest]*, with greatest likelihood between *[earliest first egg third-of-month division considering the prediction curve for the area of interest]* and *[latest nest departure third-of-month division considering the prediction curve for the area of interest]*. In general, uncertainty surrounding the estimated nesting dates varies by a period of up to 10 days. Before and after these dates, the probability of an active nest occurring is lower, but not null (Rousseu and Drolet, 2017b). This nesting period was generated from predictive models based mainly on the mean annual temperature and mainly using nest records from Project NestWatch (BSC, 2013).

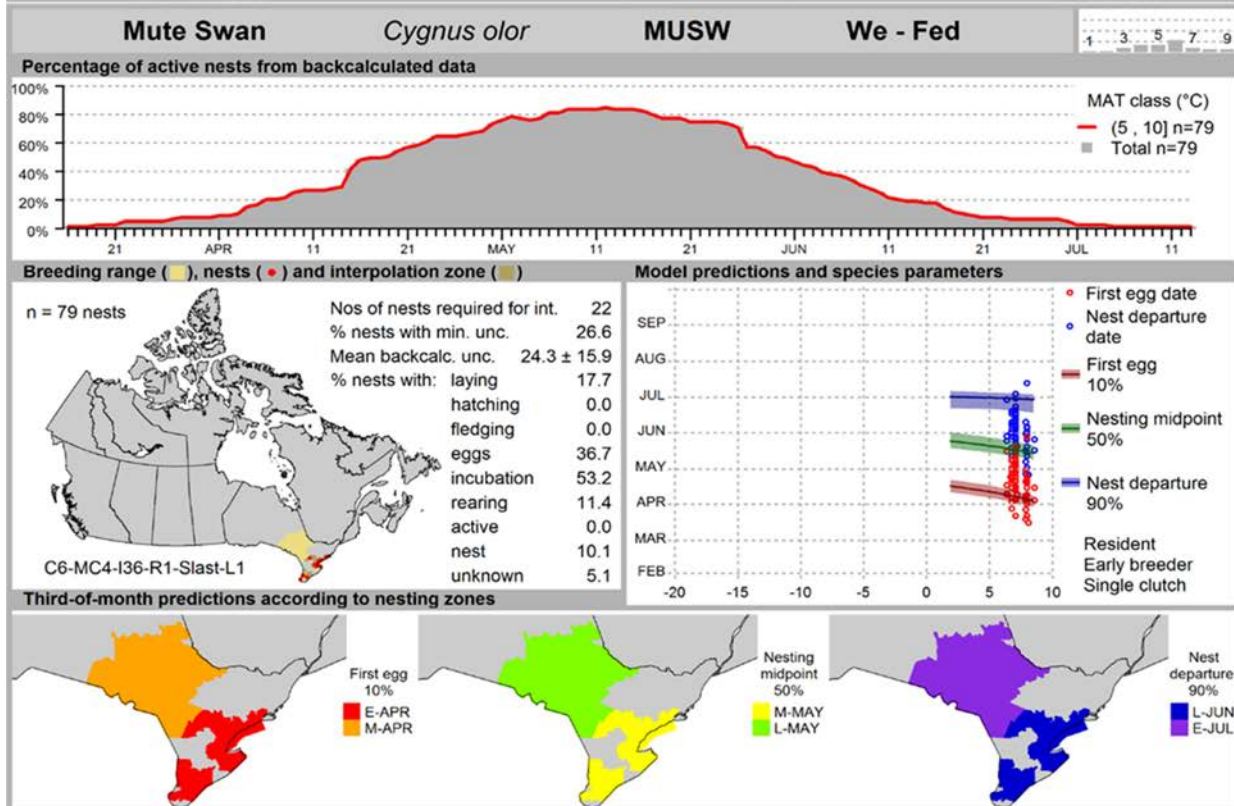
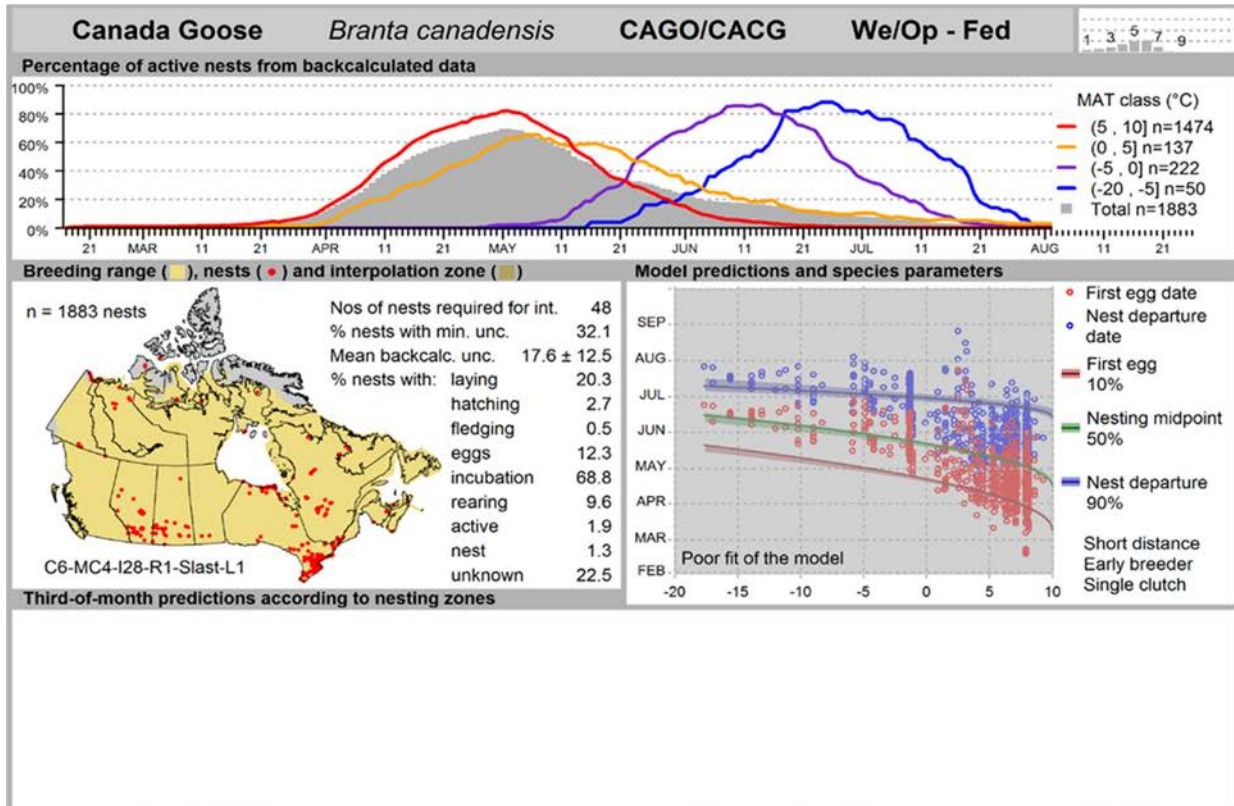
Example 4 – Description of a general nesting period when the region of interest is located in the extrapolation area

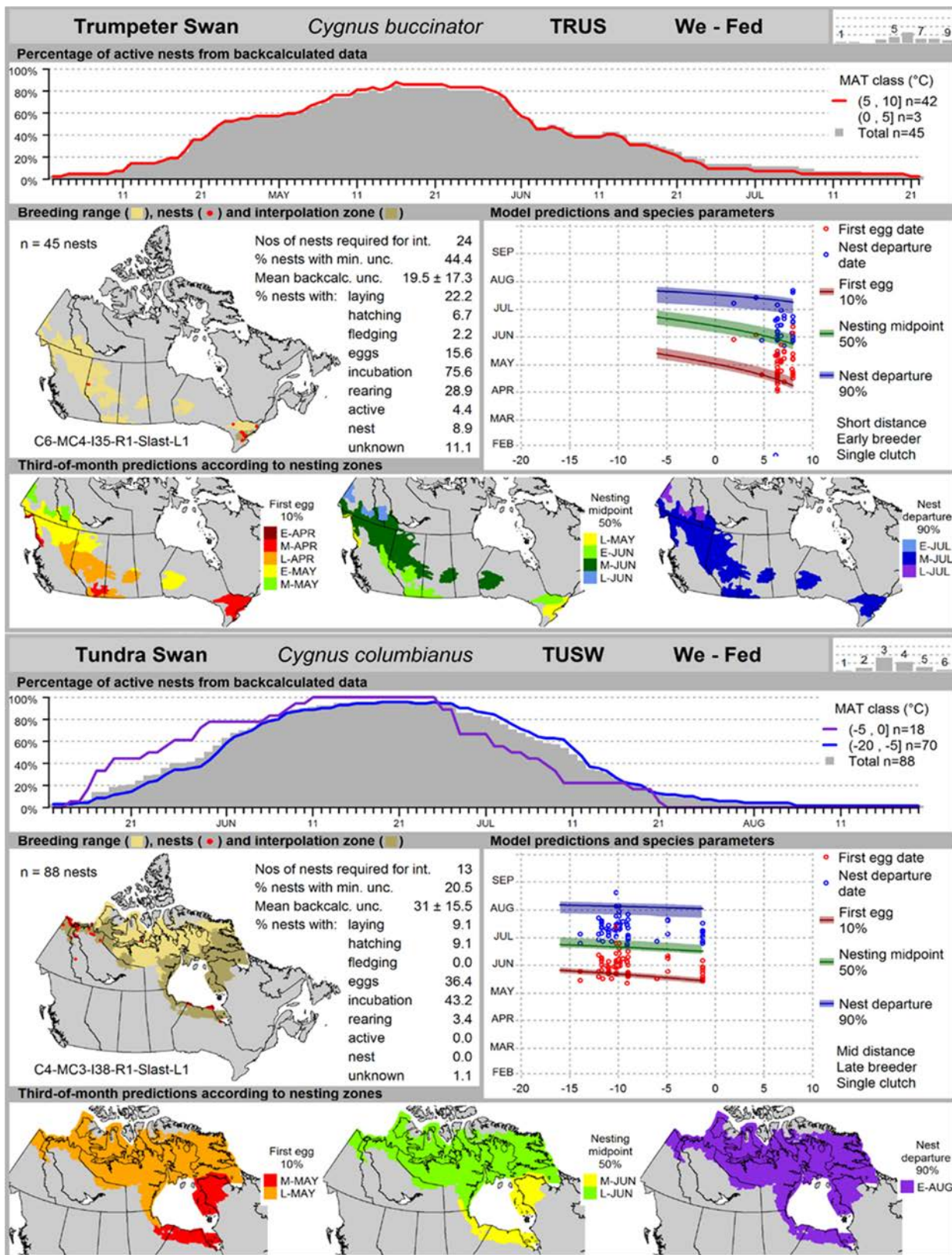
In *[region of interest]*, the general nesting period of the *[species name]*, which covers the period from the laying of first eggs up until the moment when the young have naturally left the vicinity of the nest, may start as early as *[earliest first egg third-of-month division for the area of interest]* and may extend up until *[latest nest departure third-of-month division for the area of interest]*. In general, uncertainty surrounding the estimated nesting dates varies by a period of up to 10 days. Before and after these dates, the probability of an active nest occurring is lower, but not null (Rousseu and Drolet, 2017b). Greater caution is advised when using predictions for this species in this area because they are based on relatively limited data. Due to a possible higher uncertainty, the predictions in this area may vary by one or more third-of-month divisions. This nesting period was generated from predictive models based mainly on the mean annual temperature and mainly using nest records from Project NestWatch (BSC, 2013).

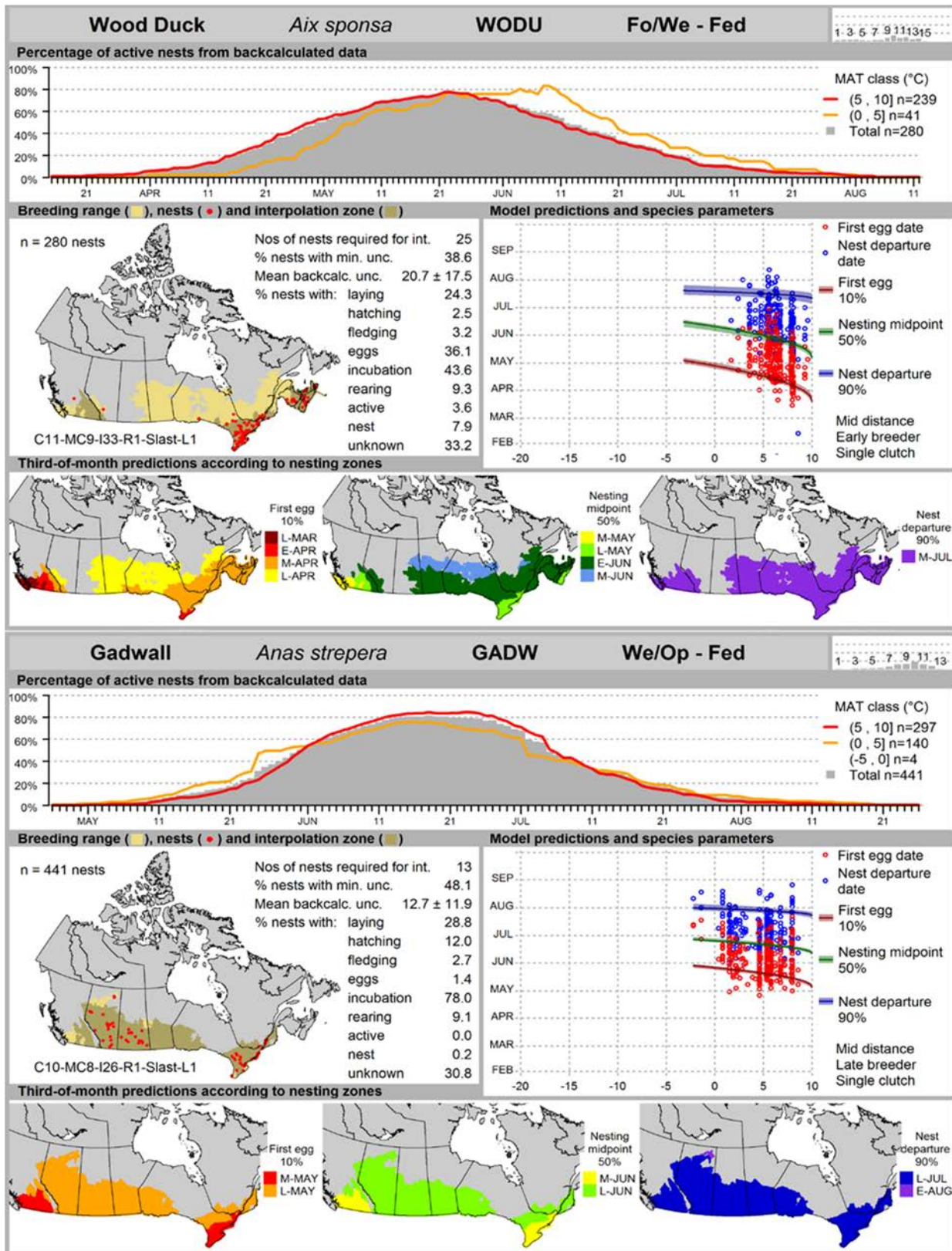
SPECIES ACCOUNTS (IN PHYLOGENETICAL ORDER)

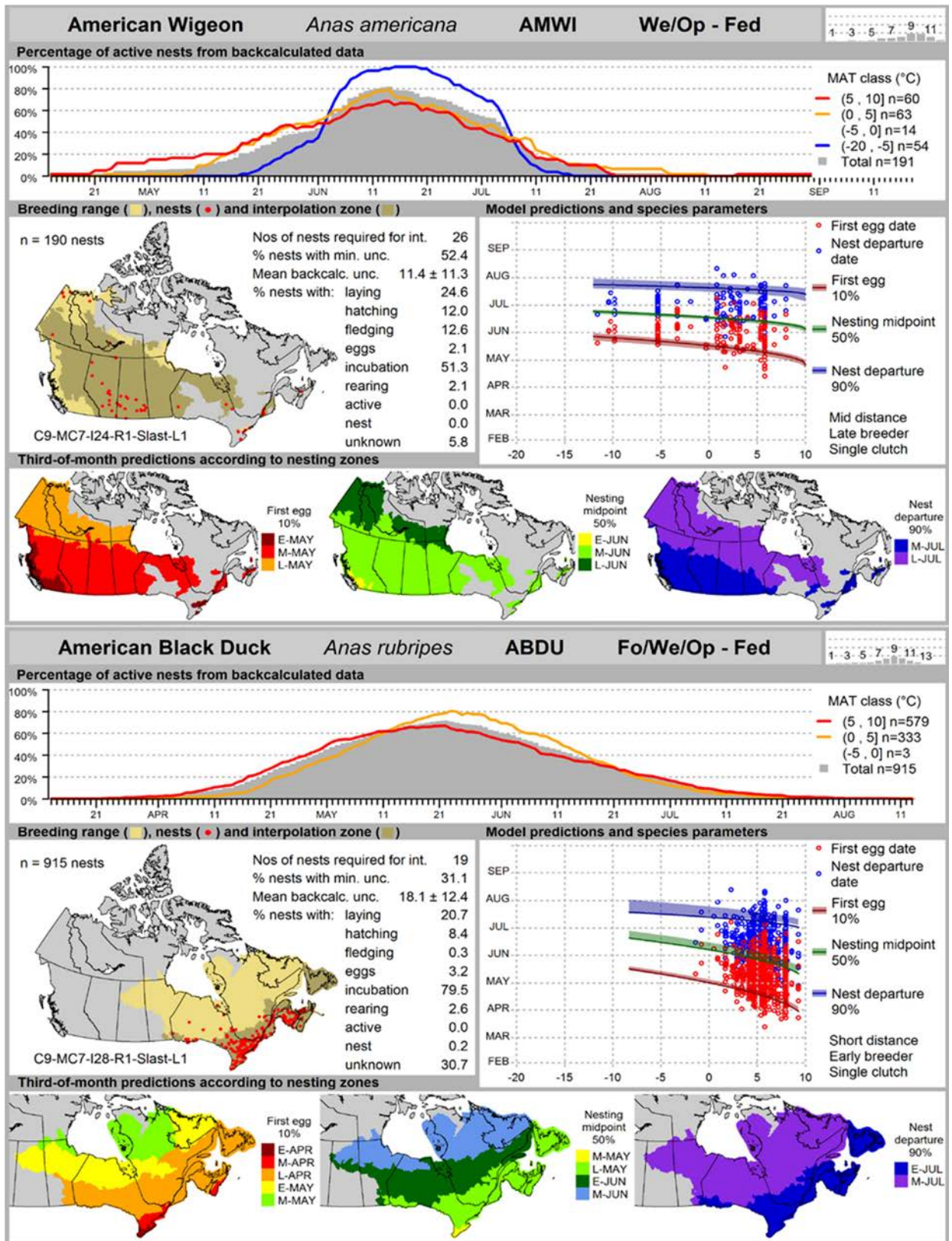


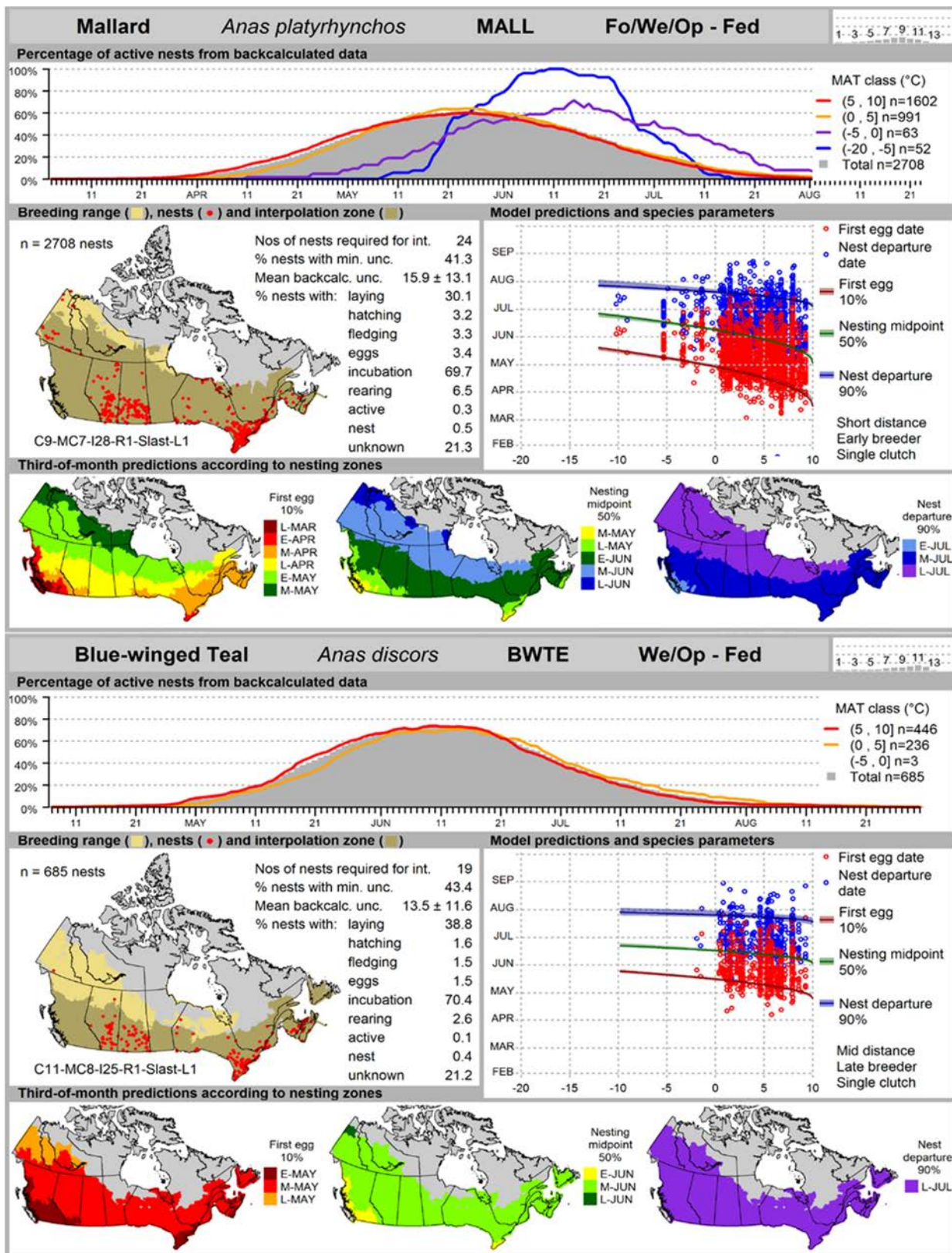


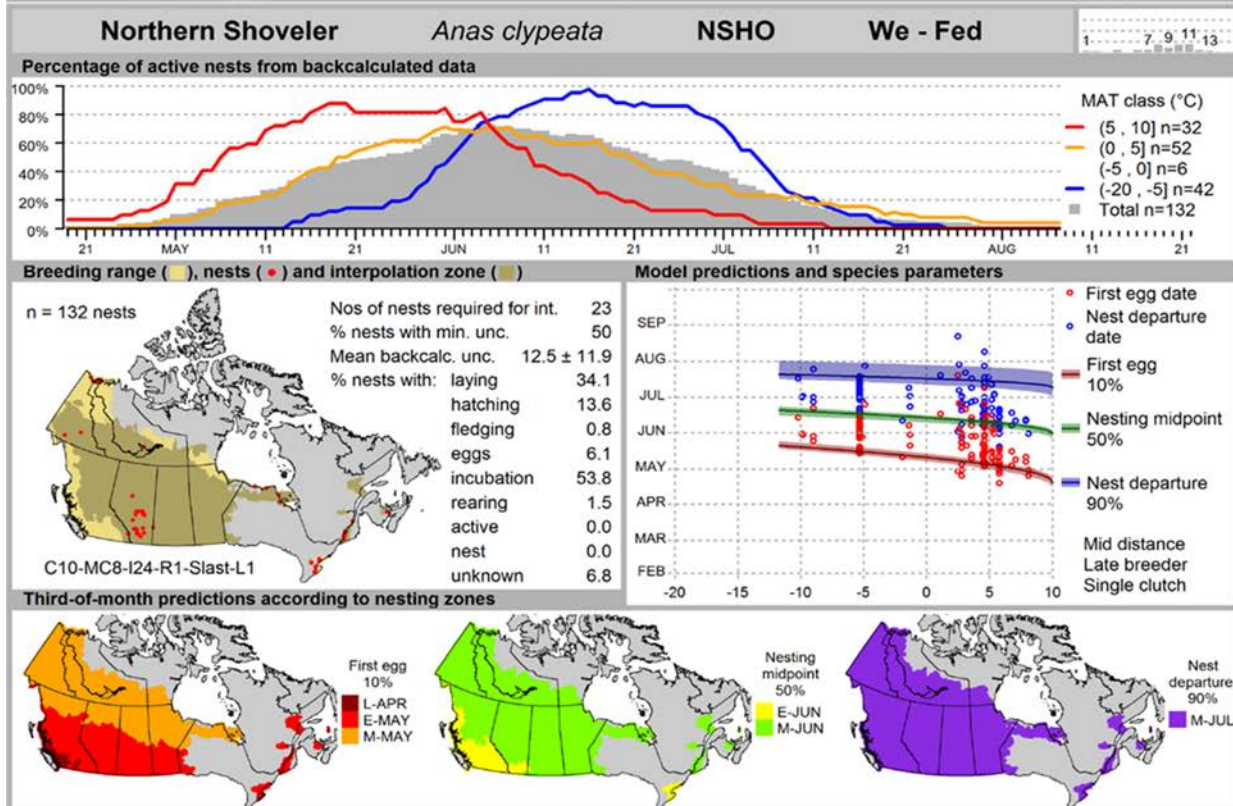
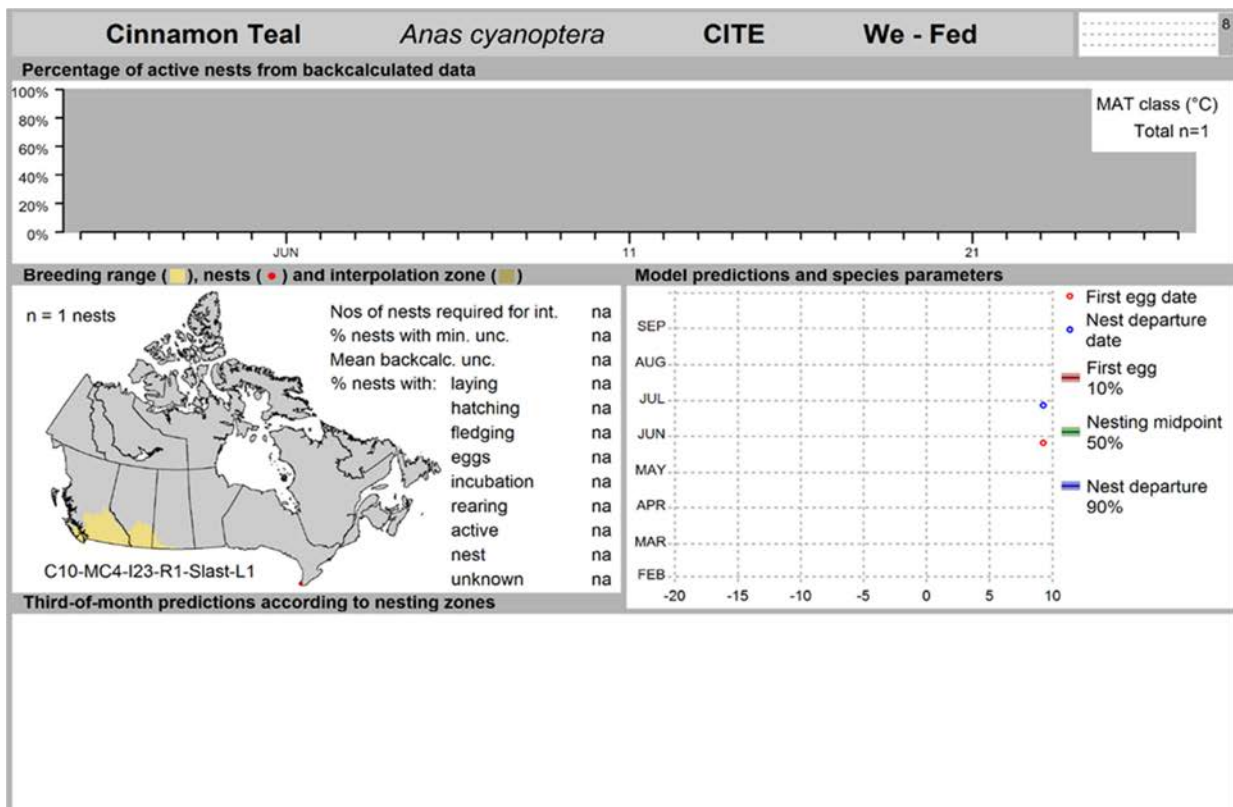


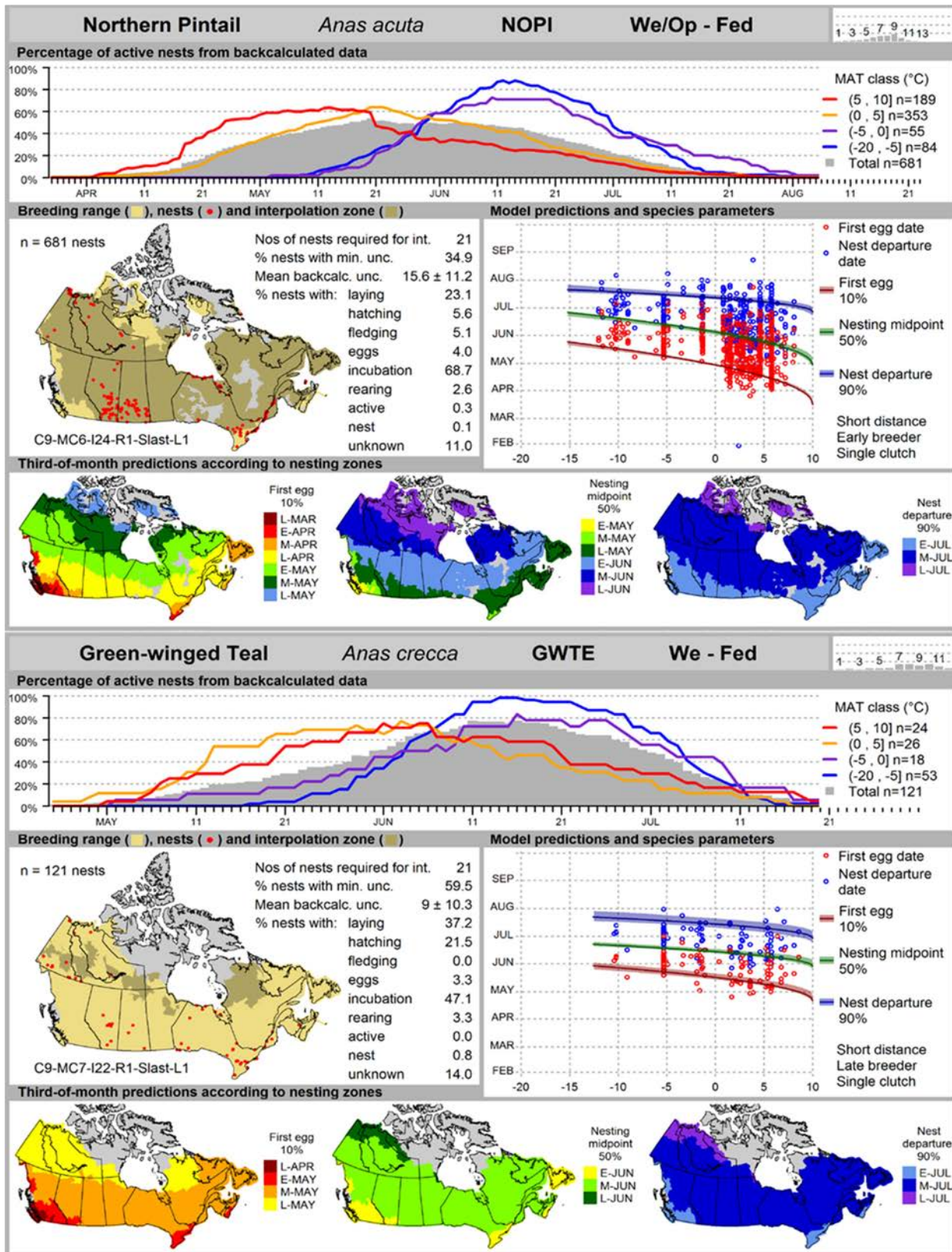


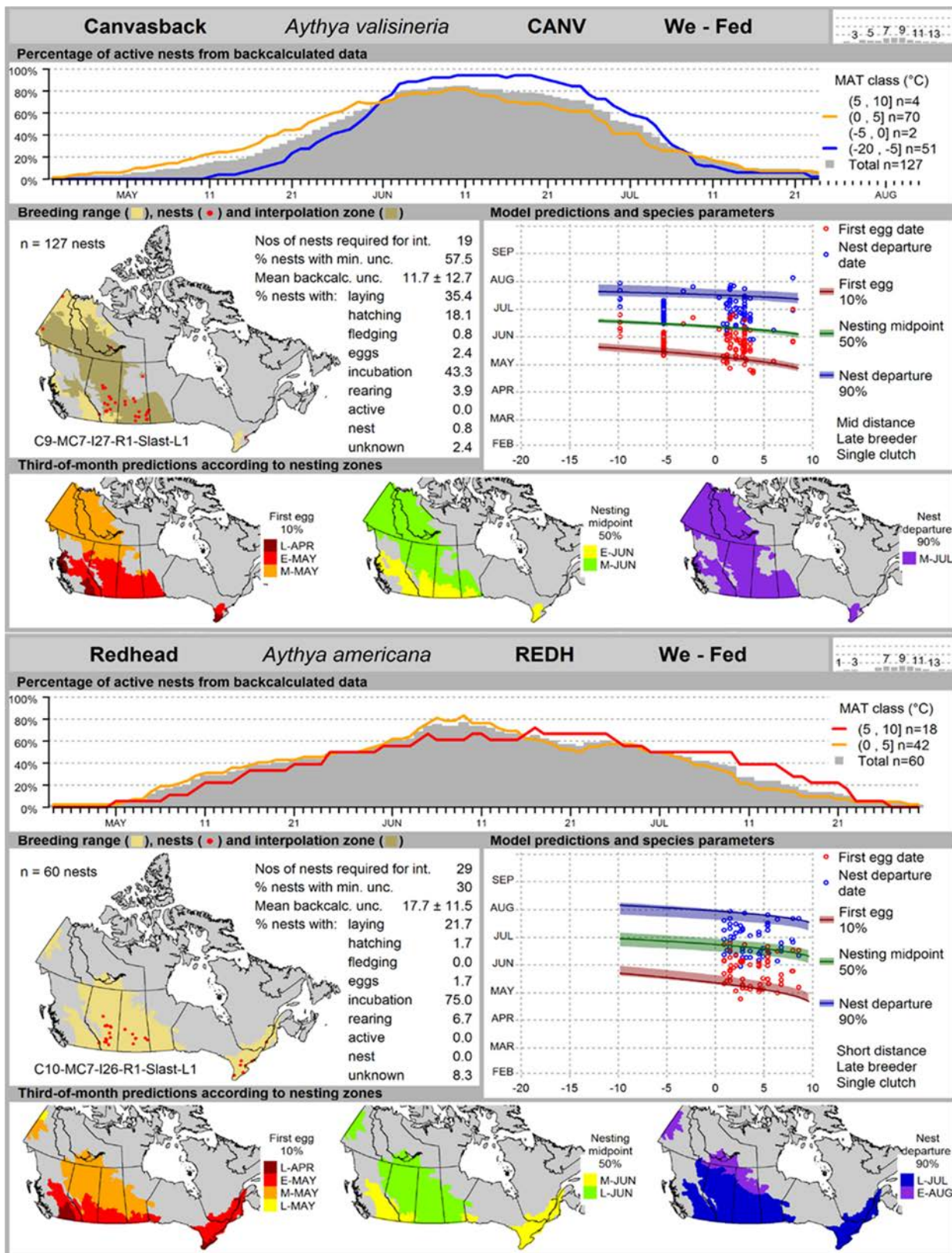


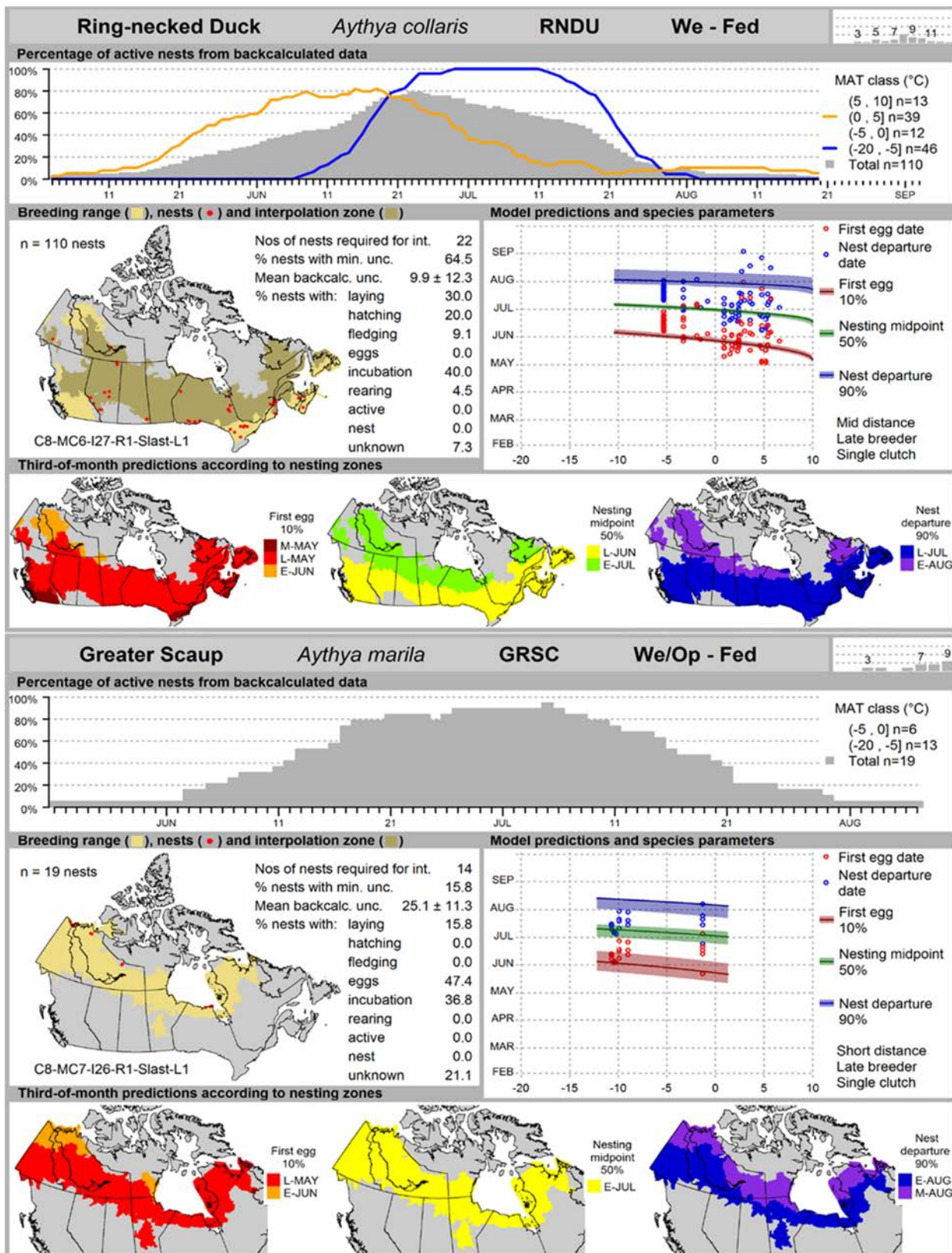


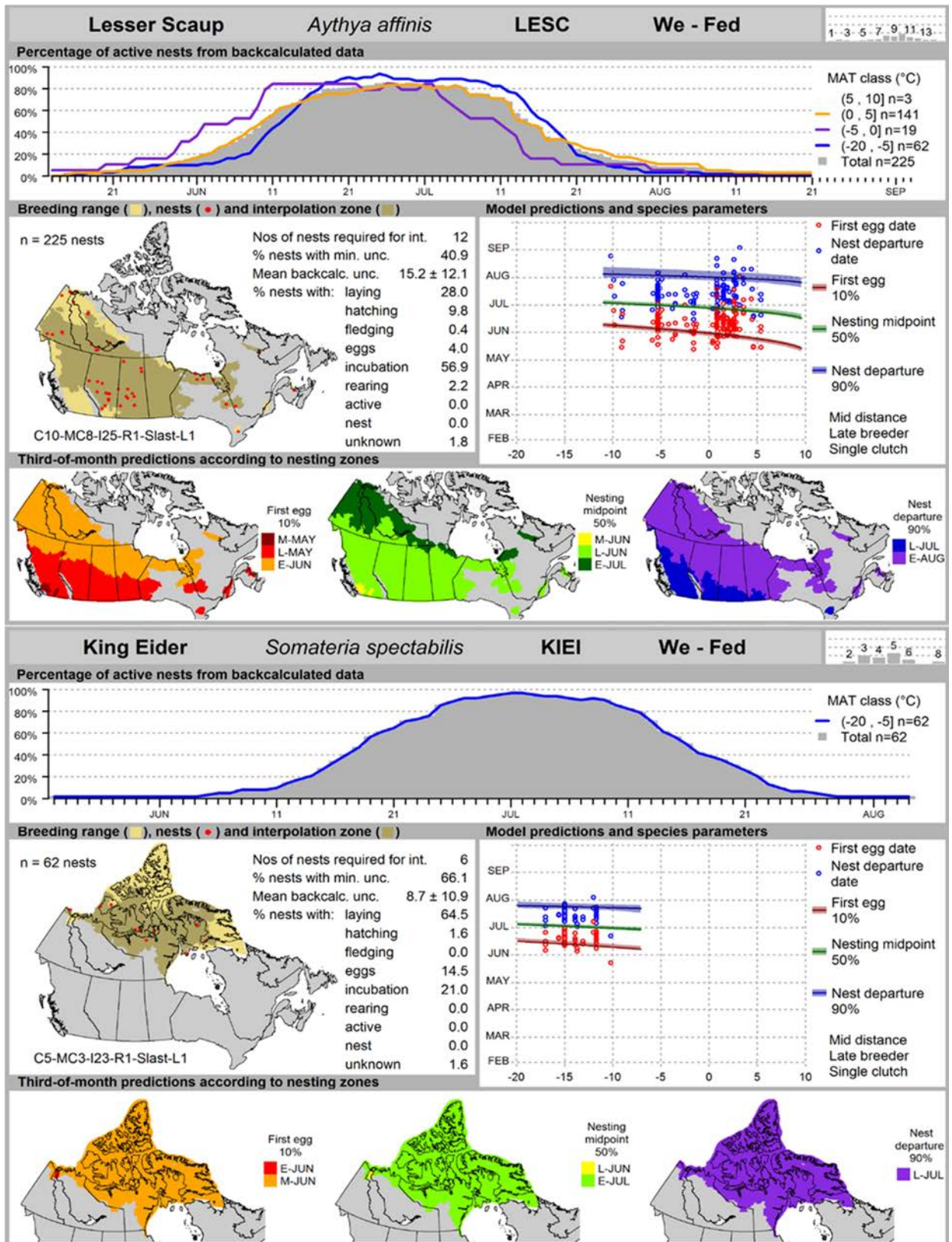


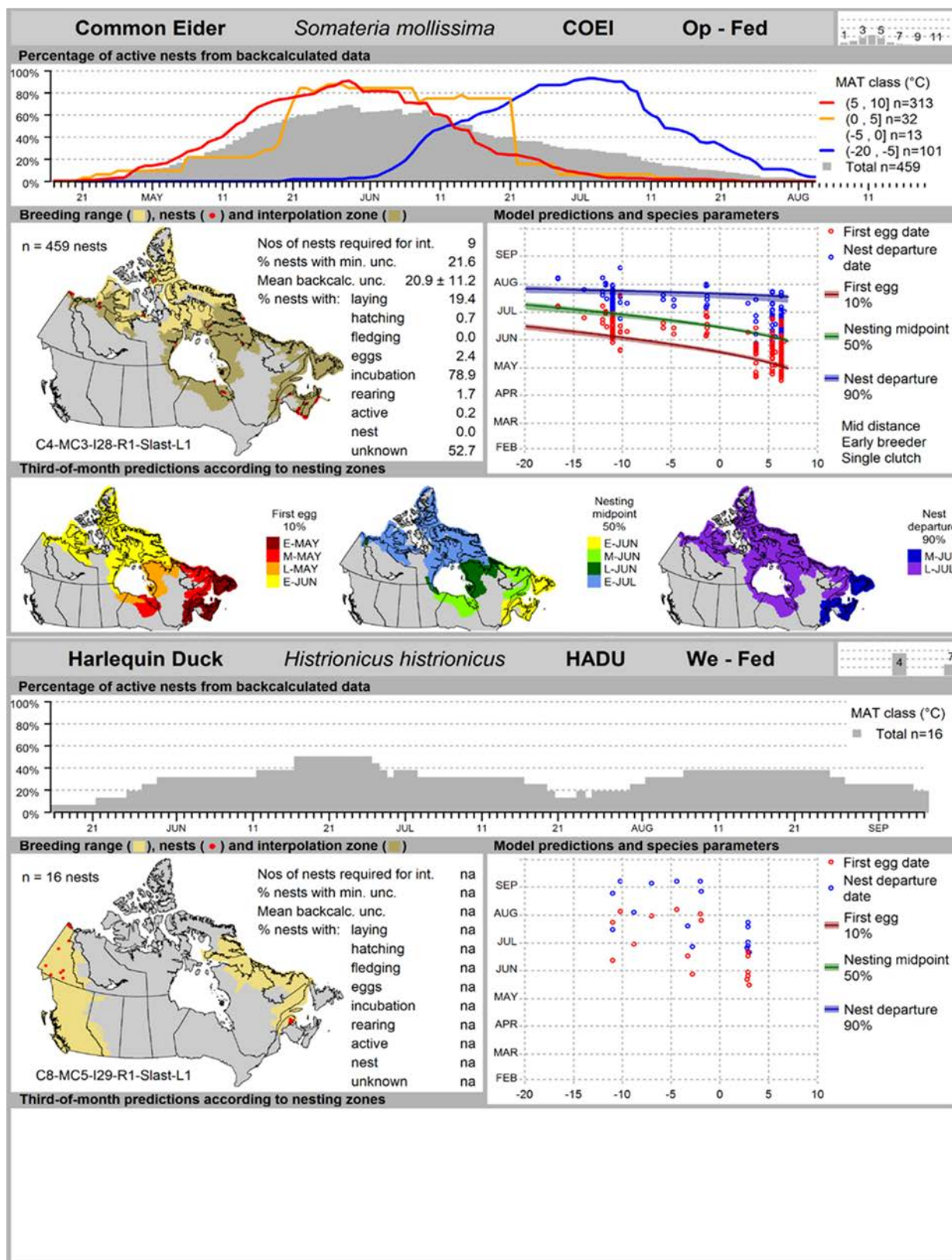


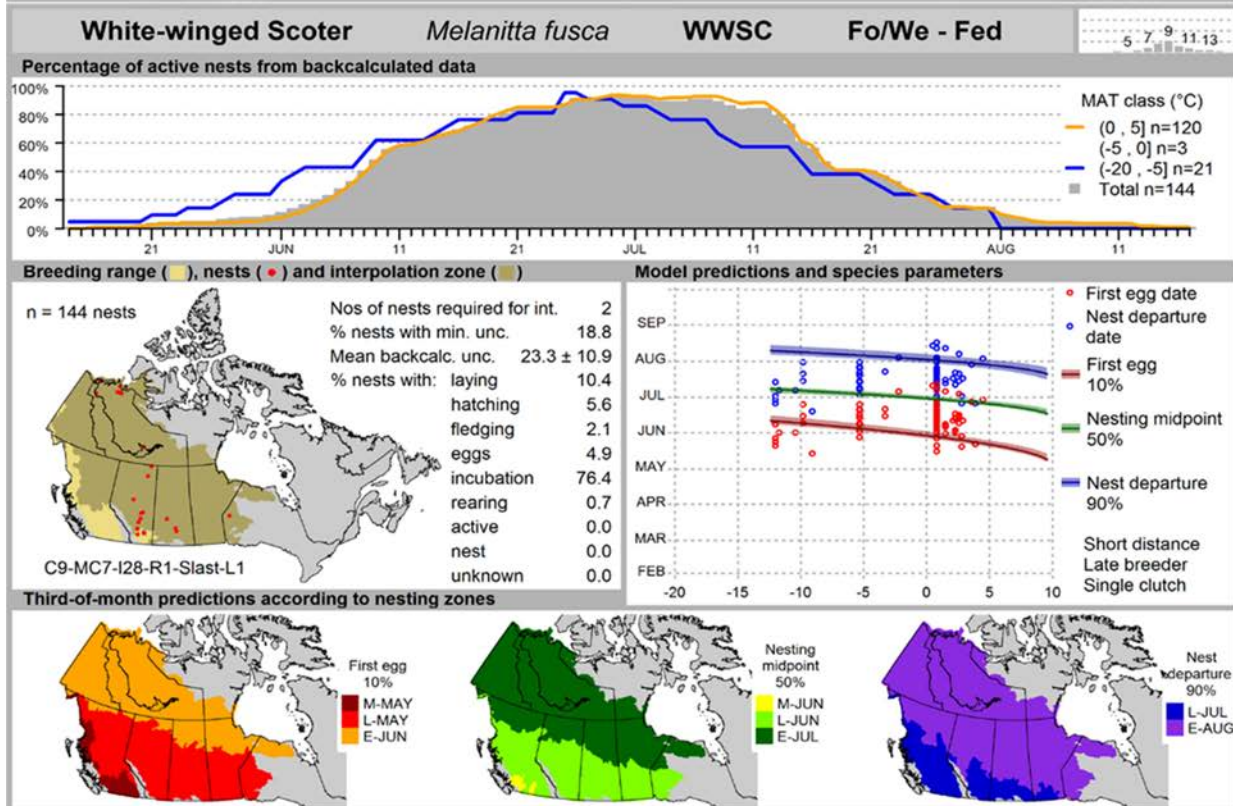
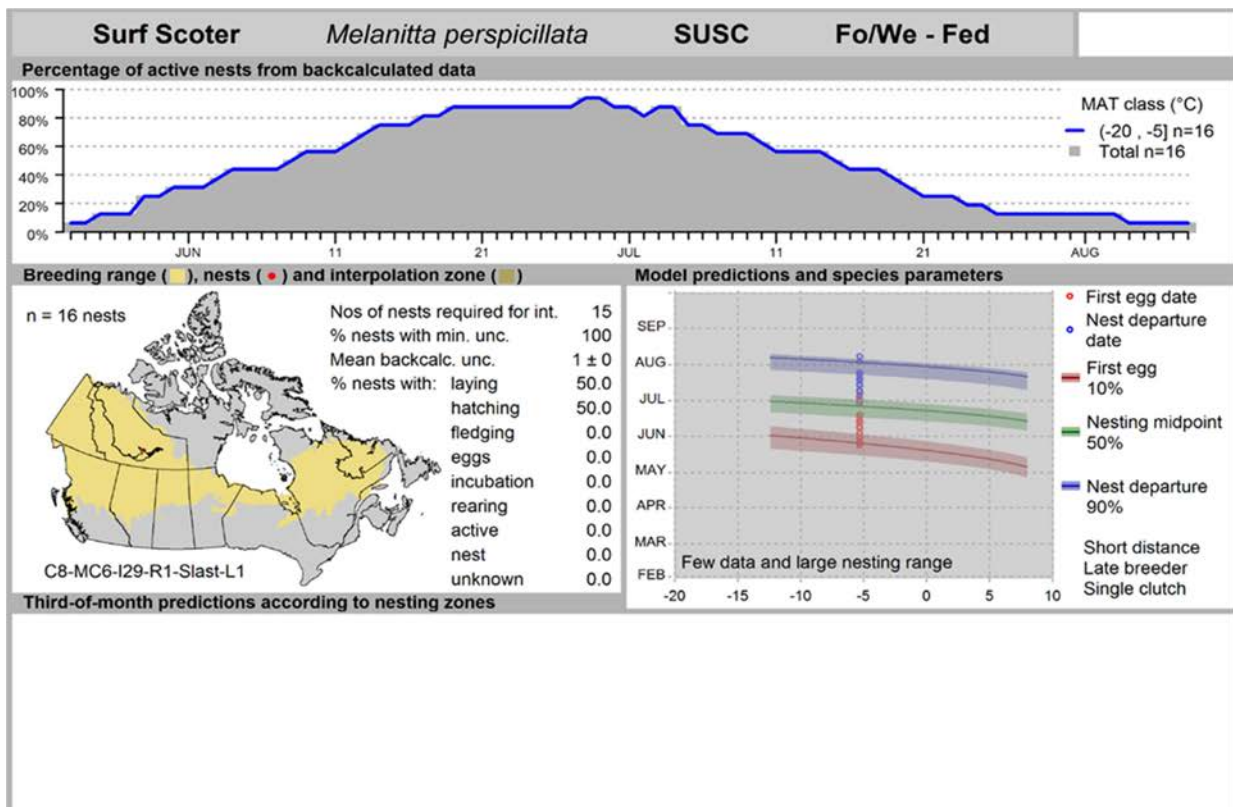


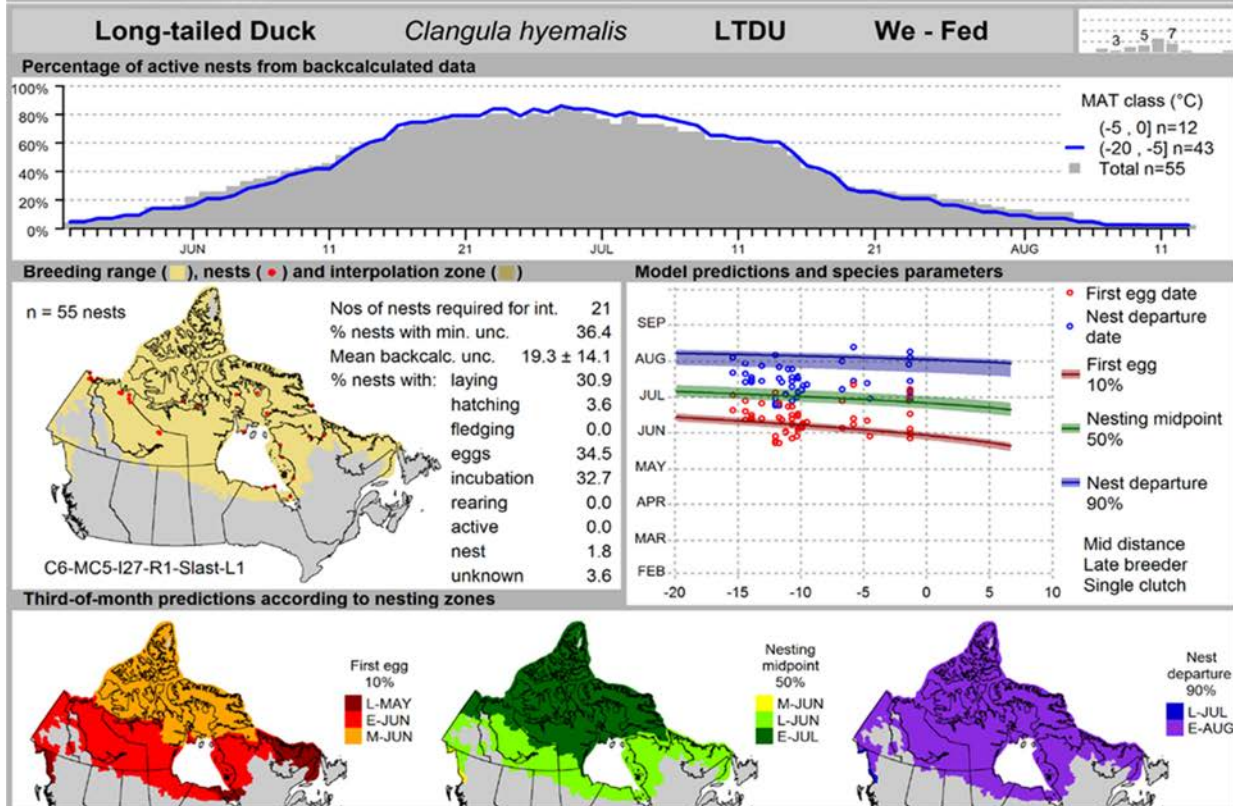
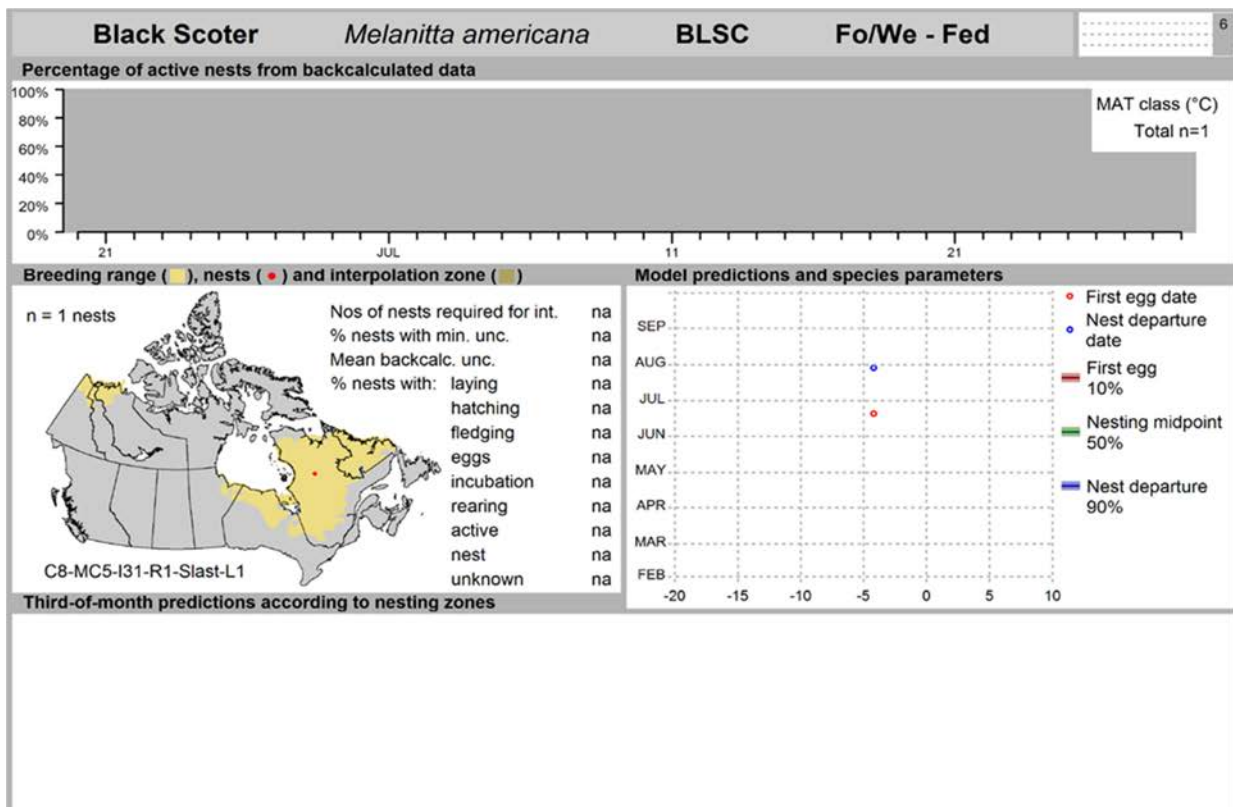


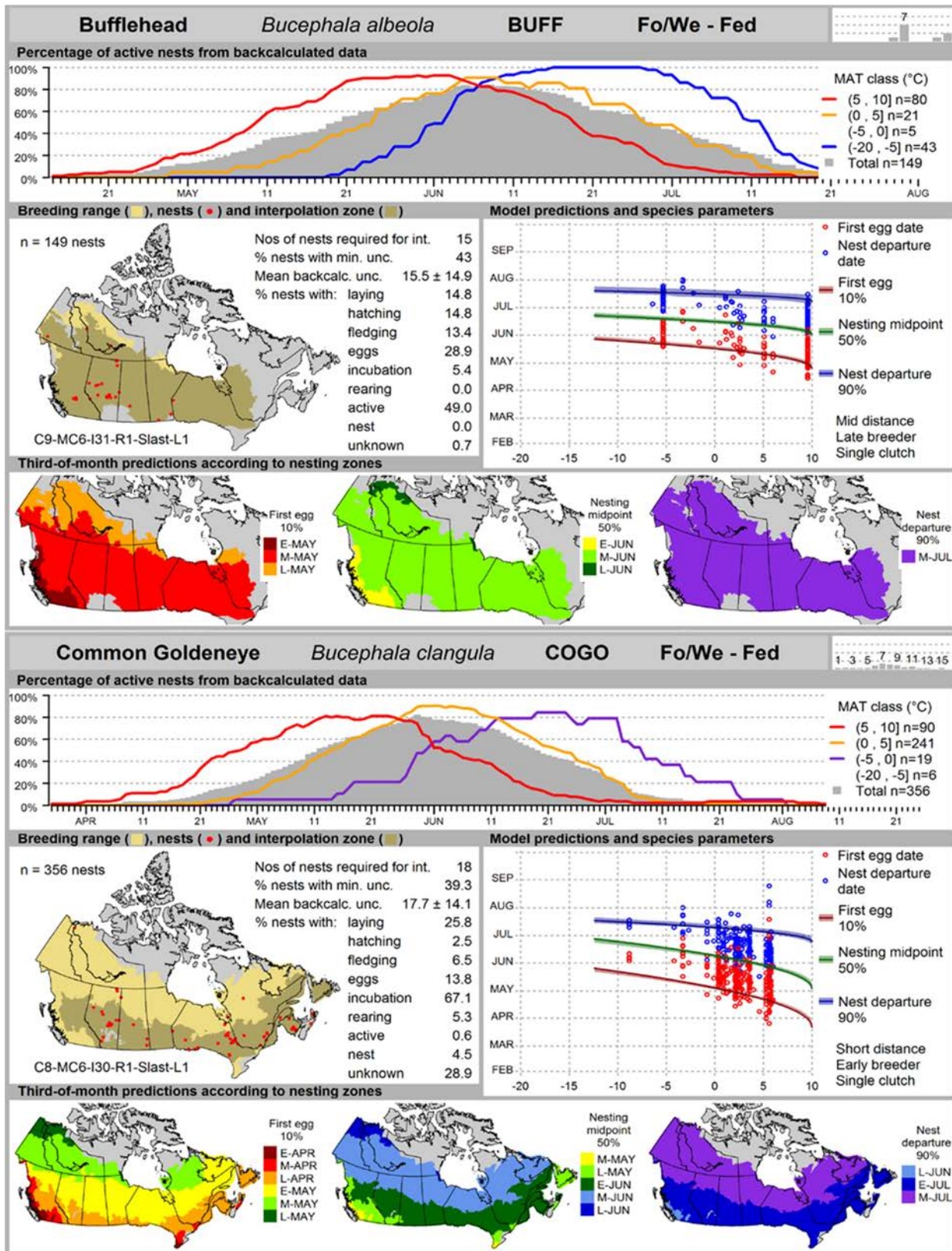


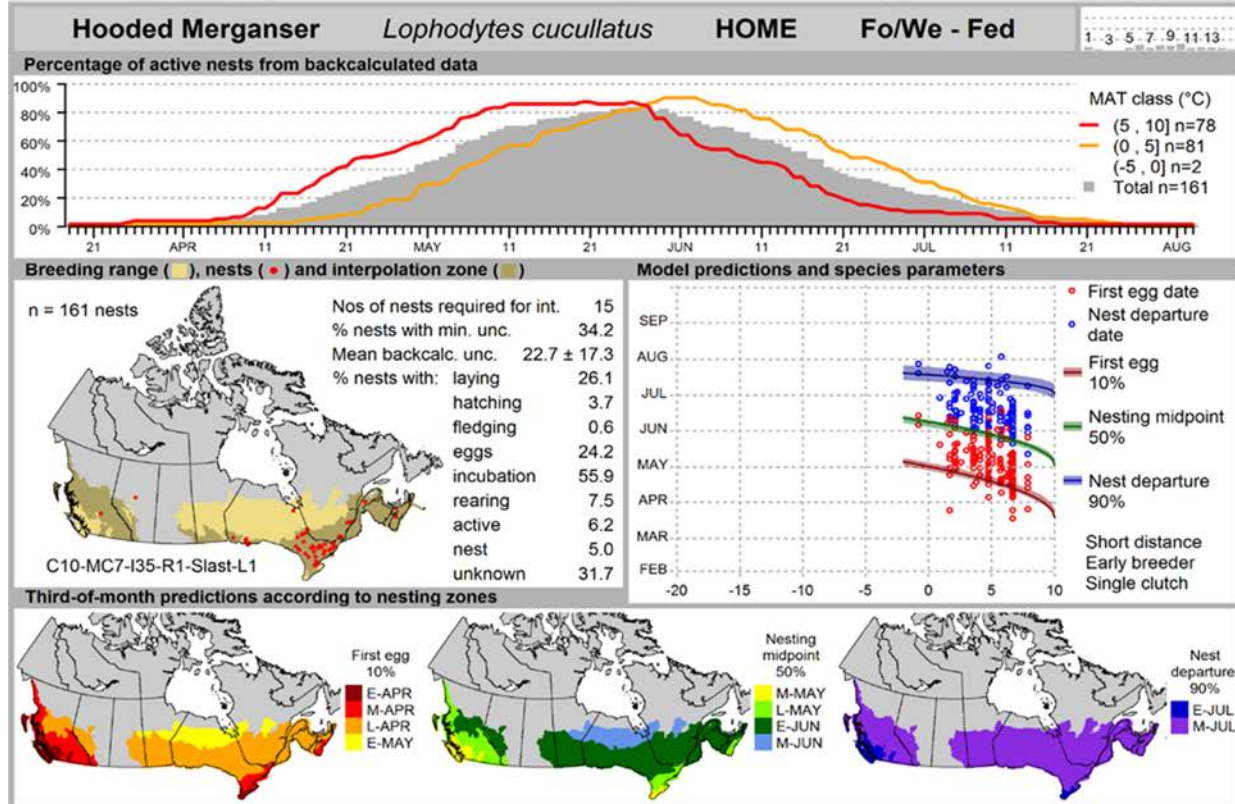
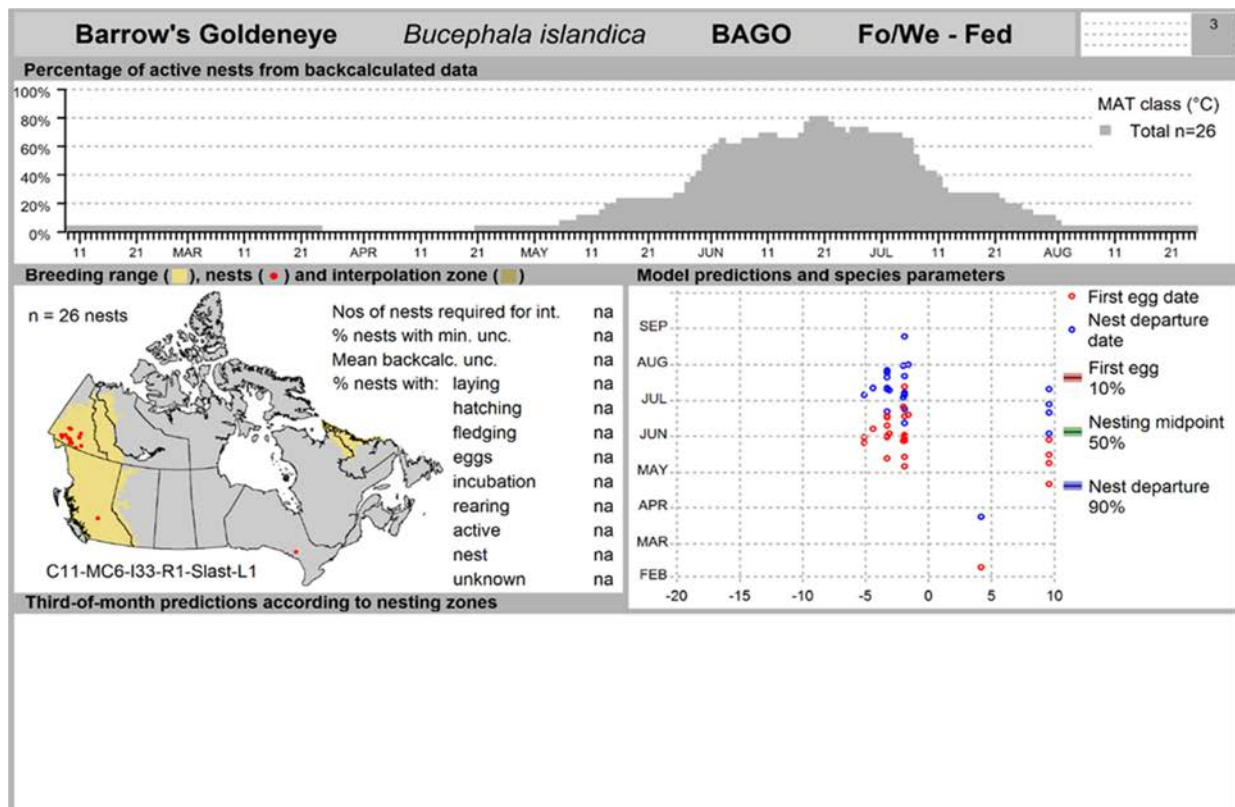


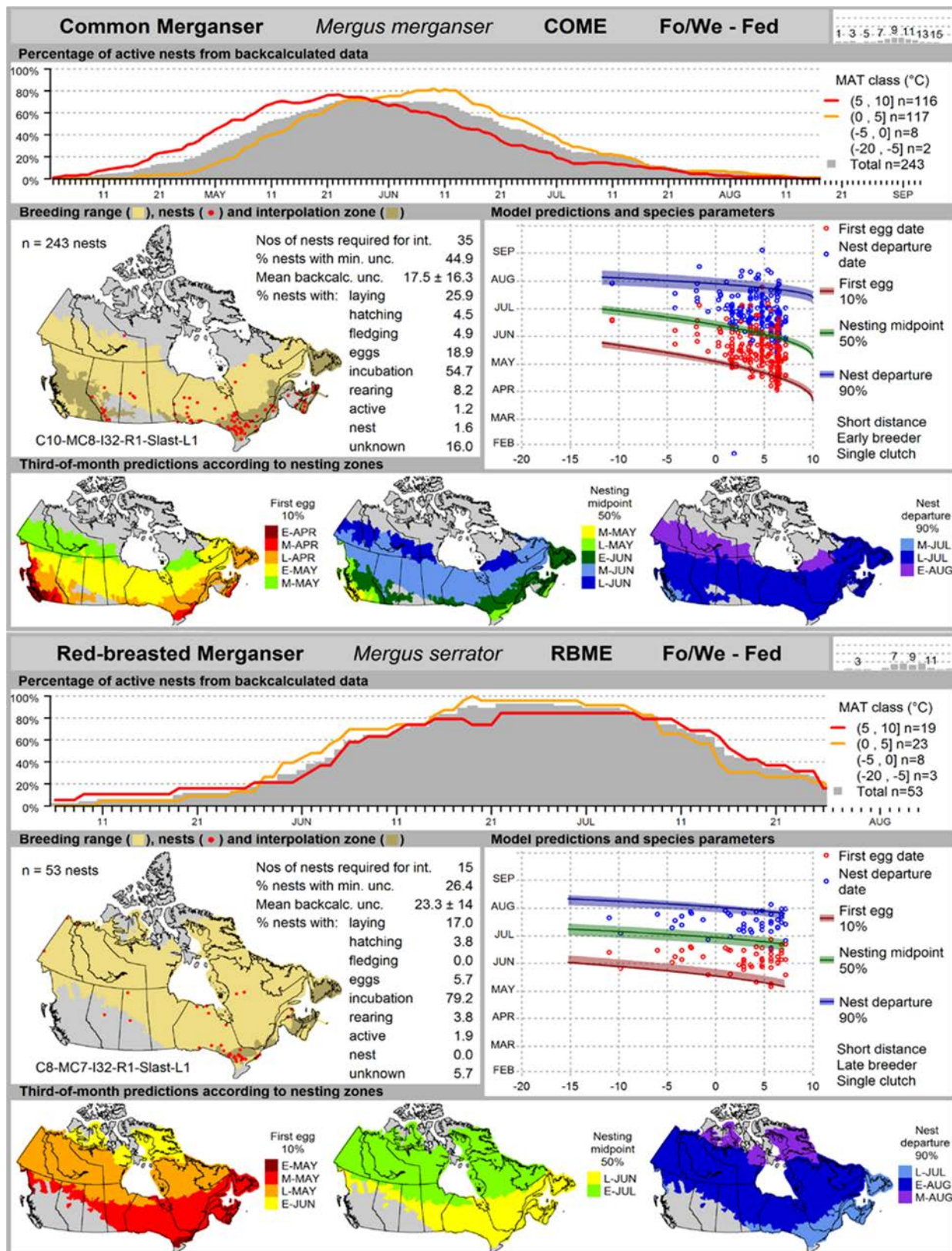


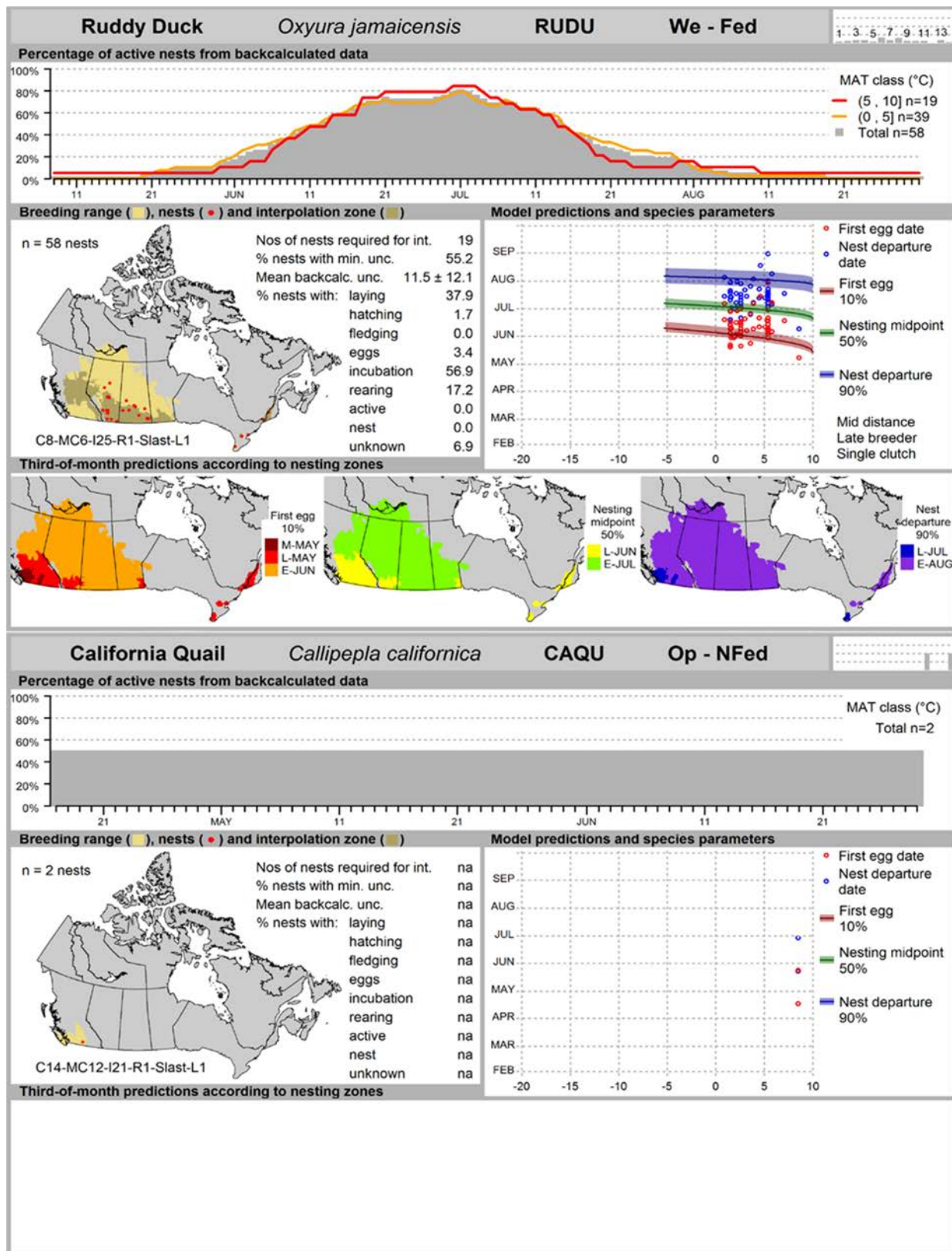


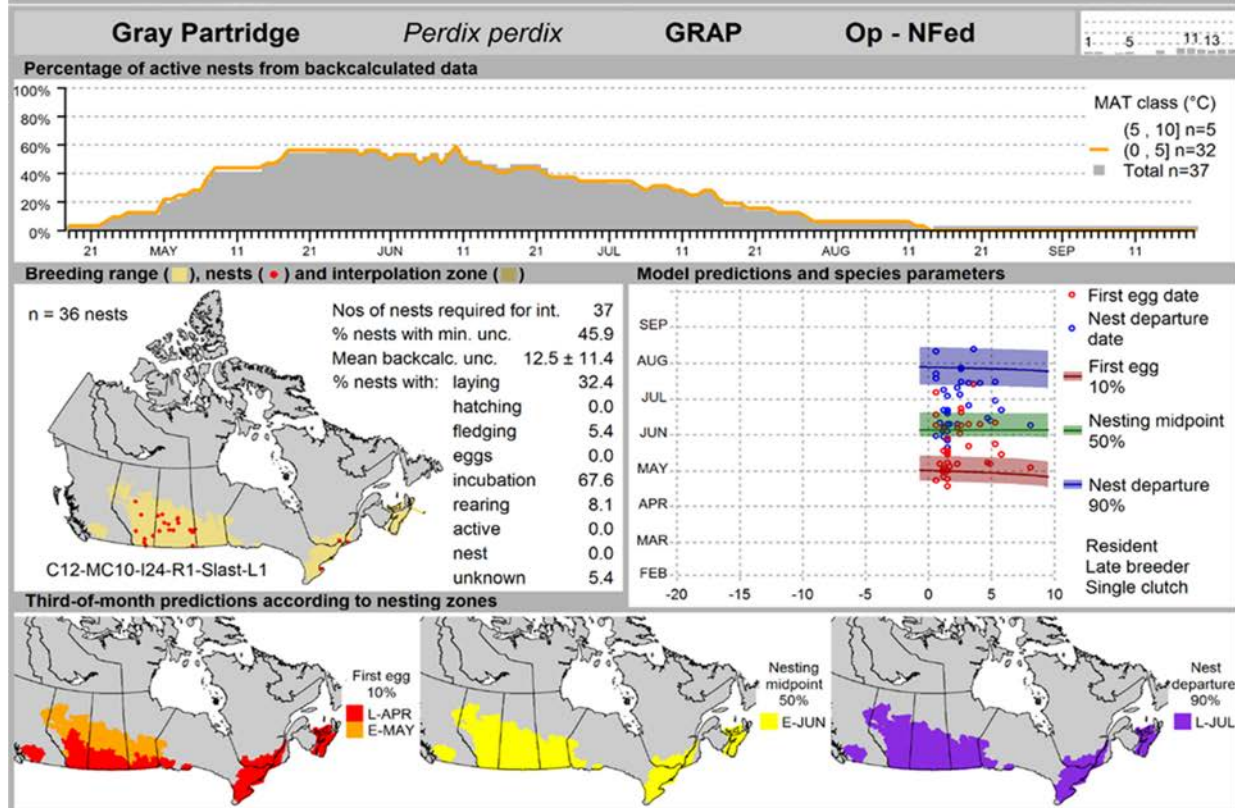
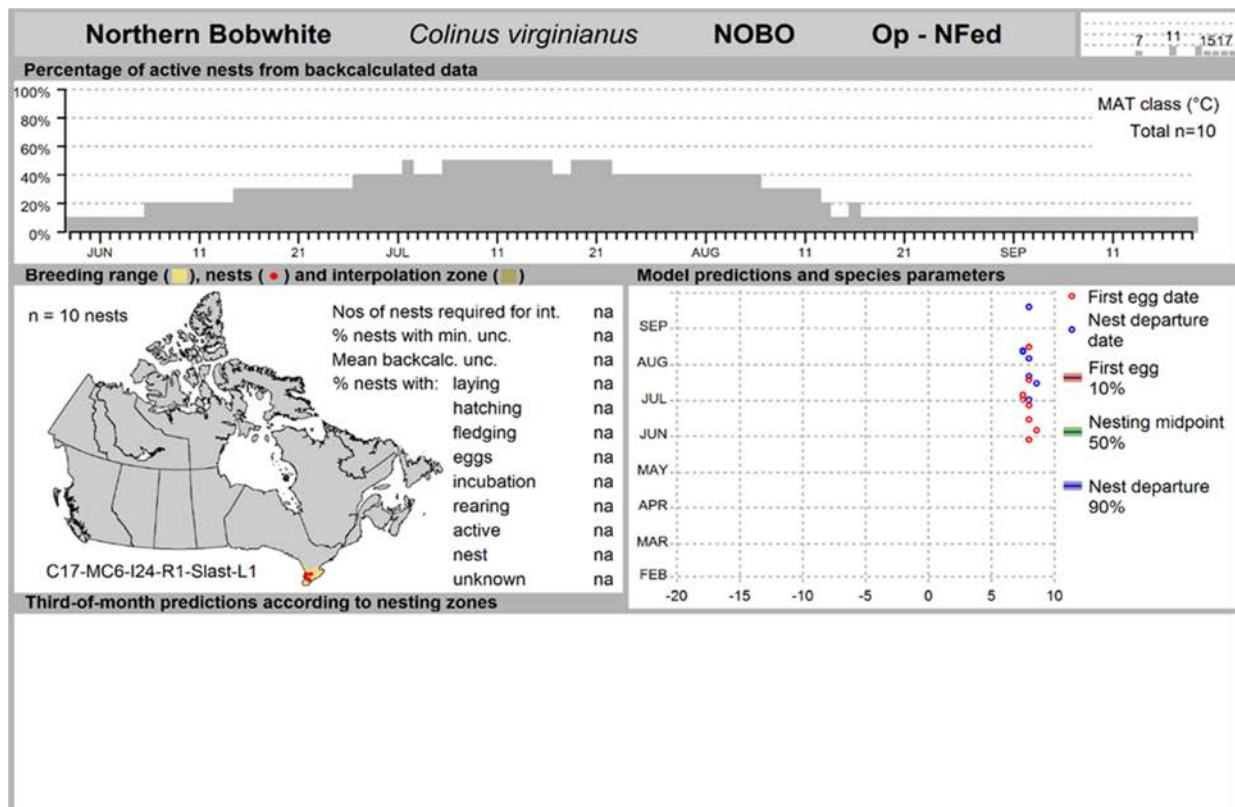


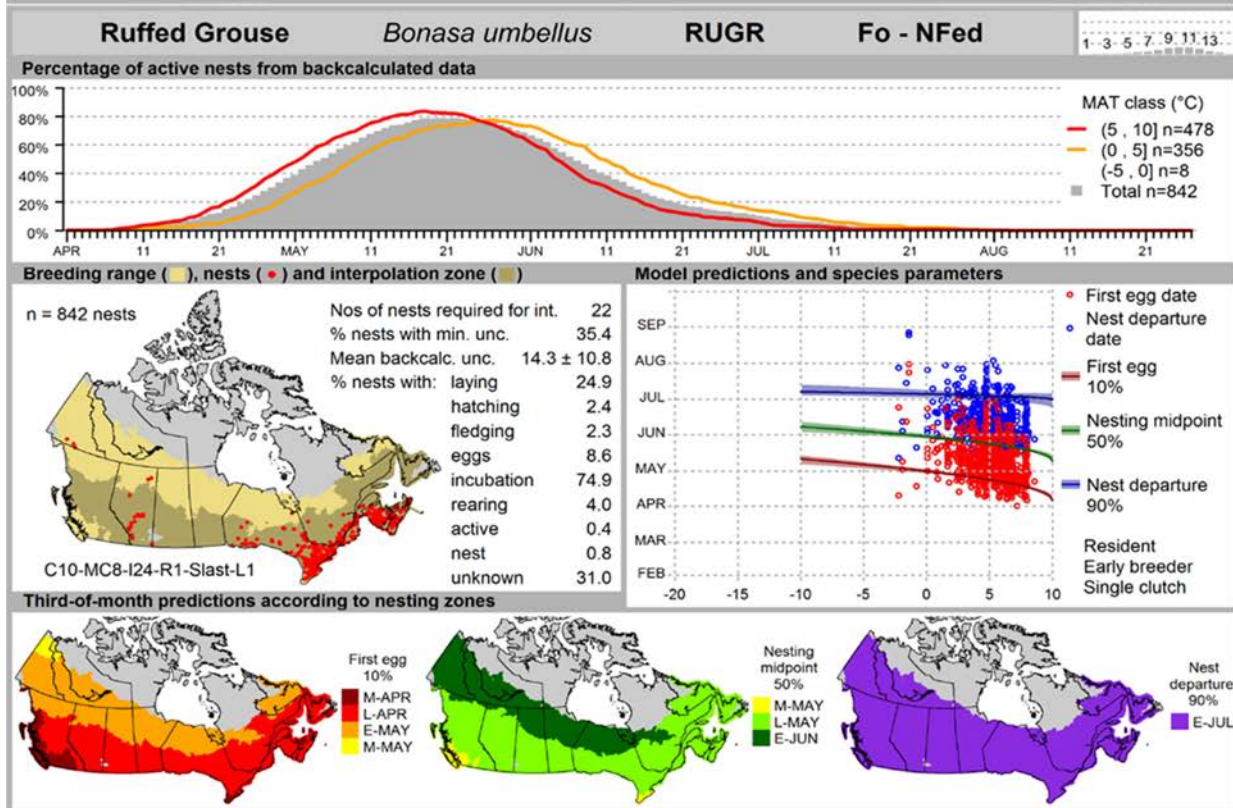
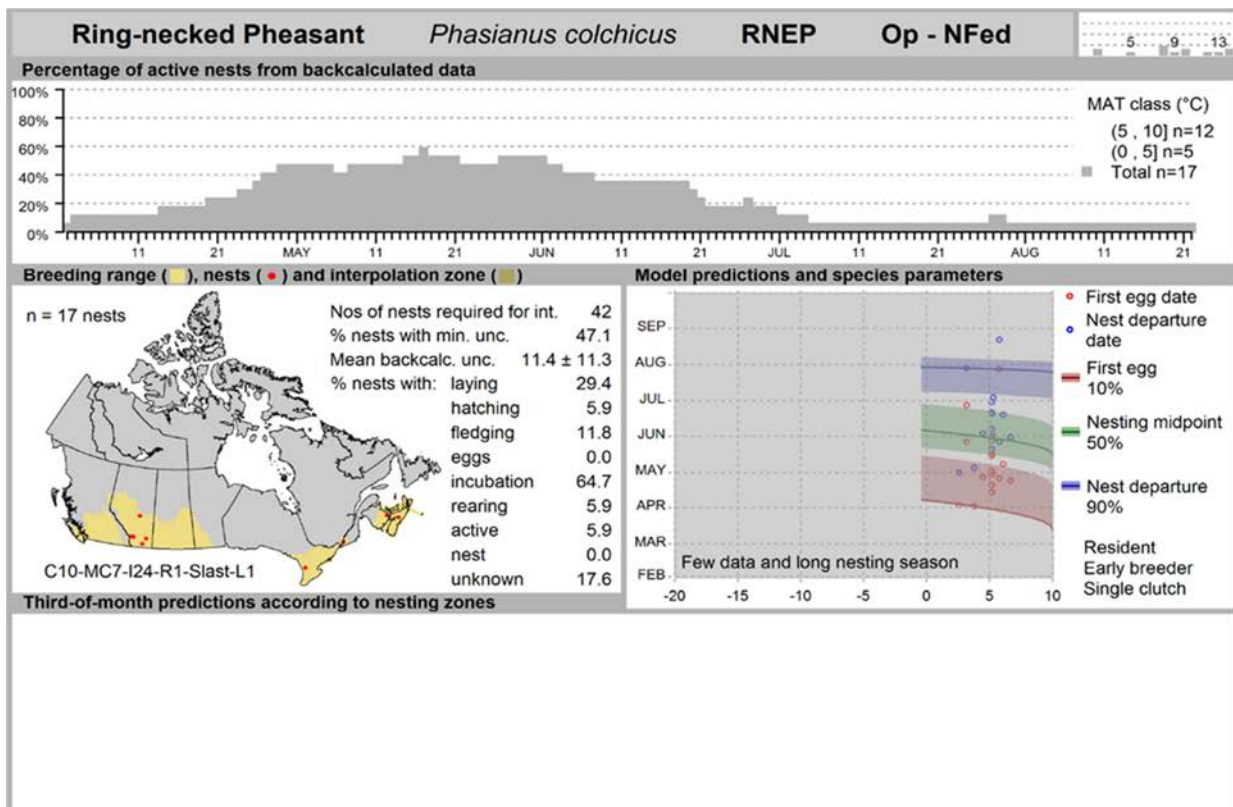


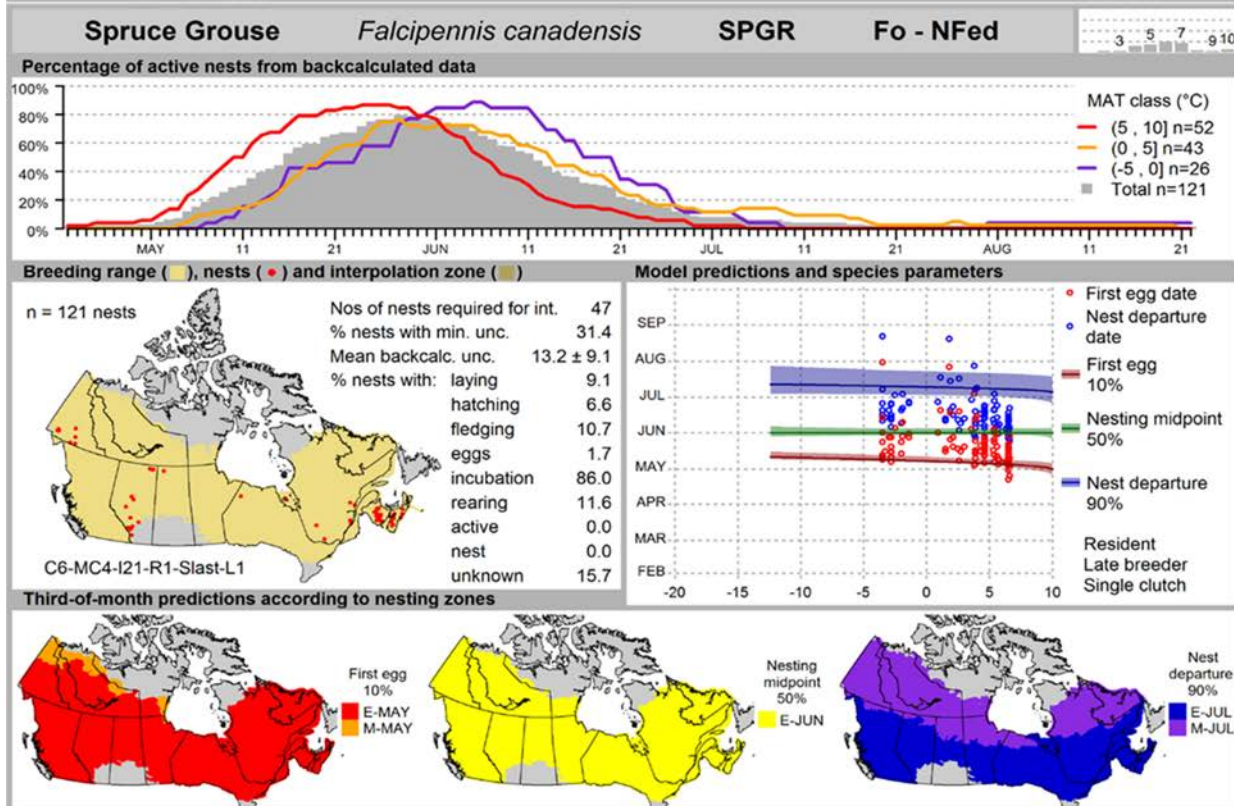
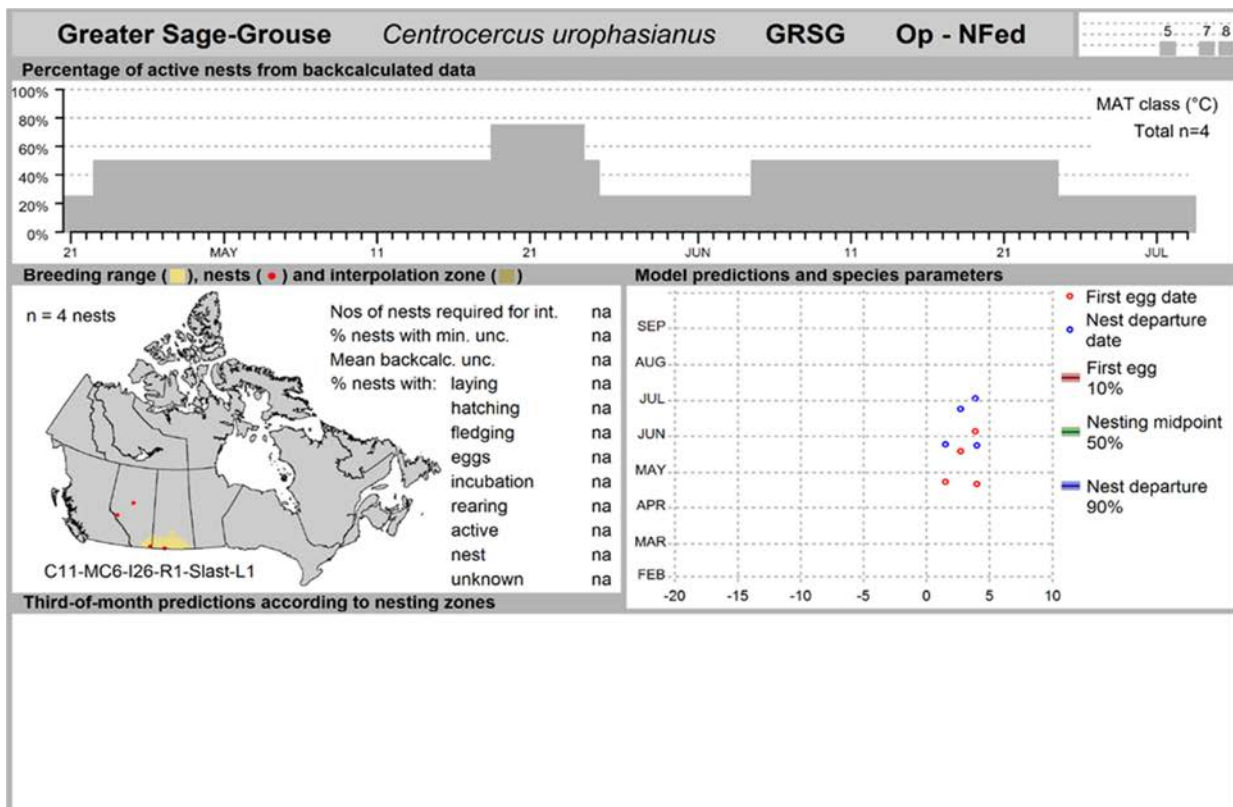


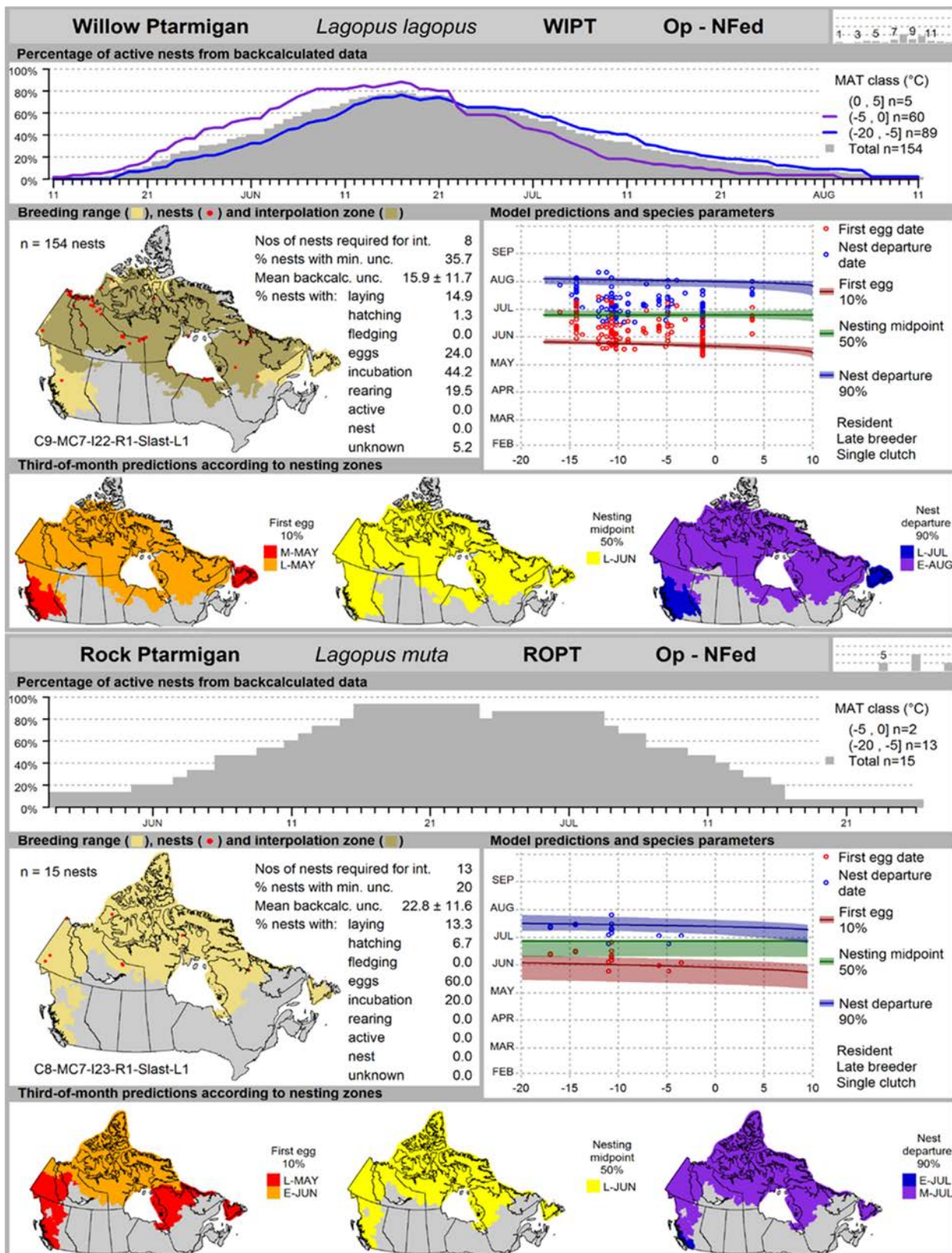


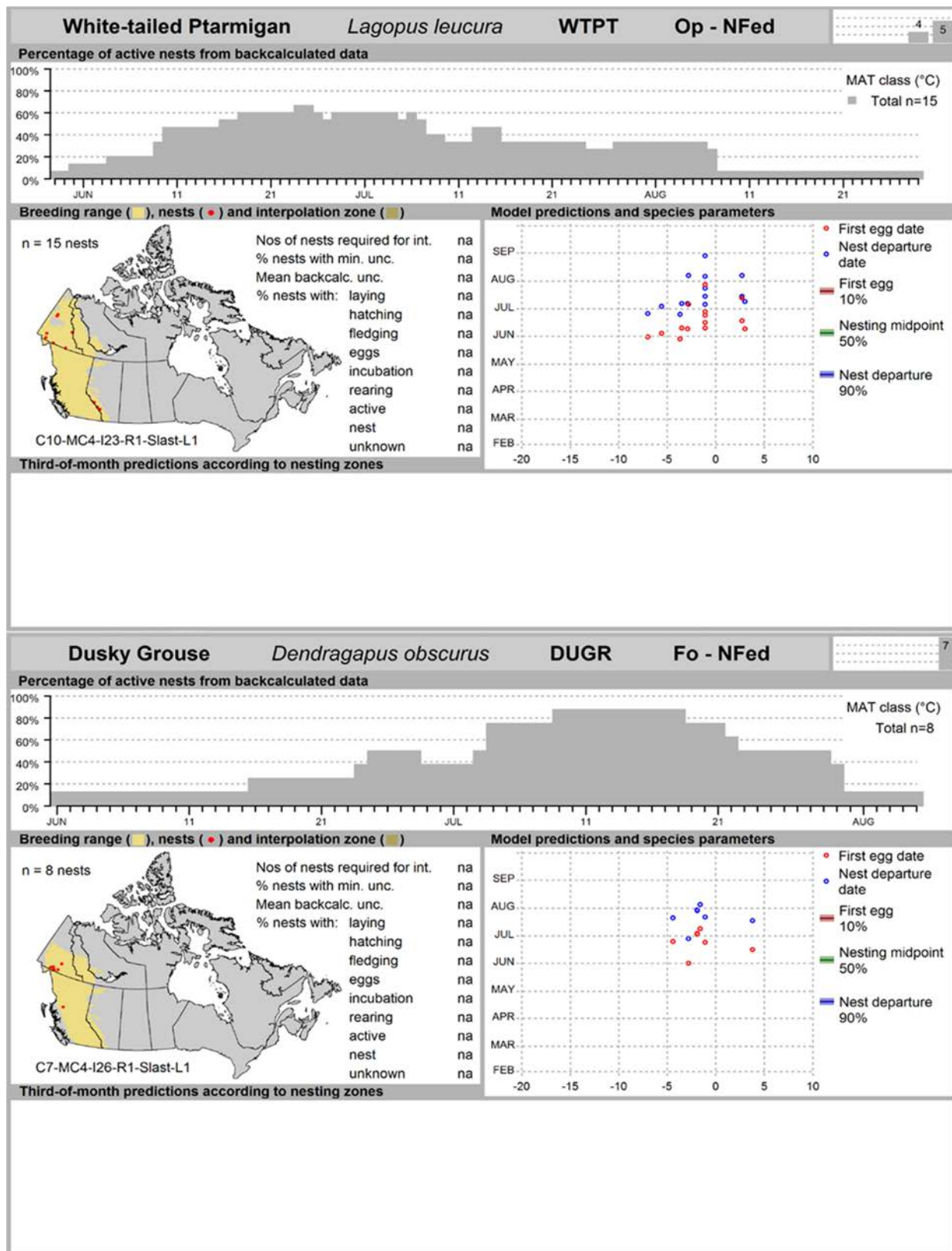


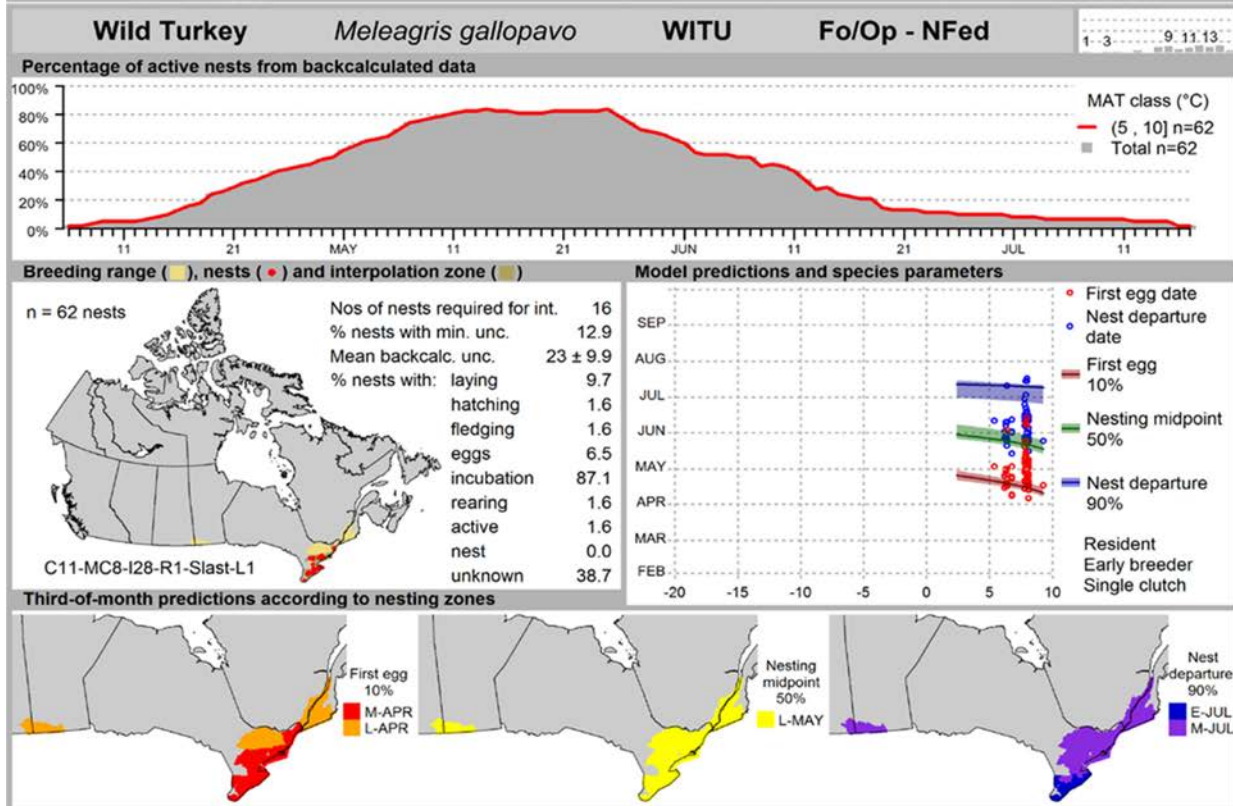
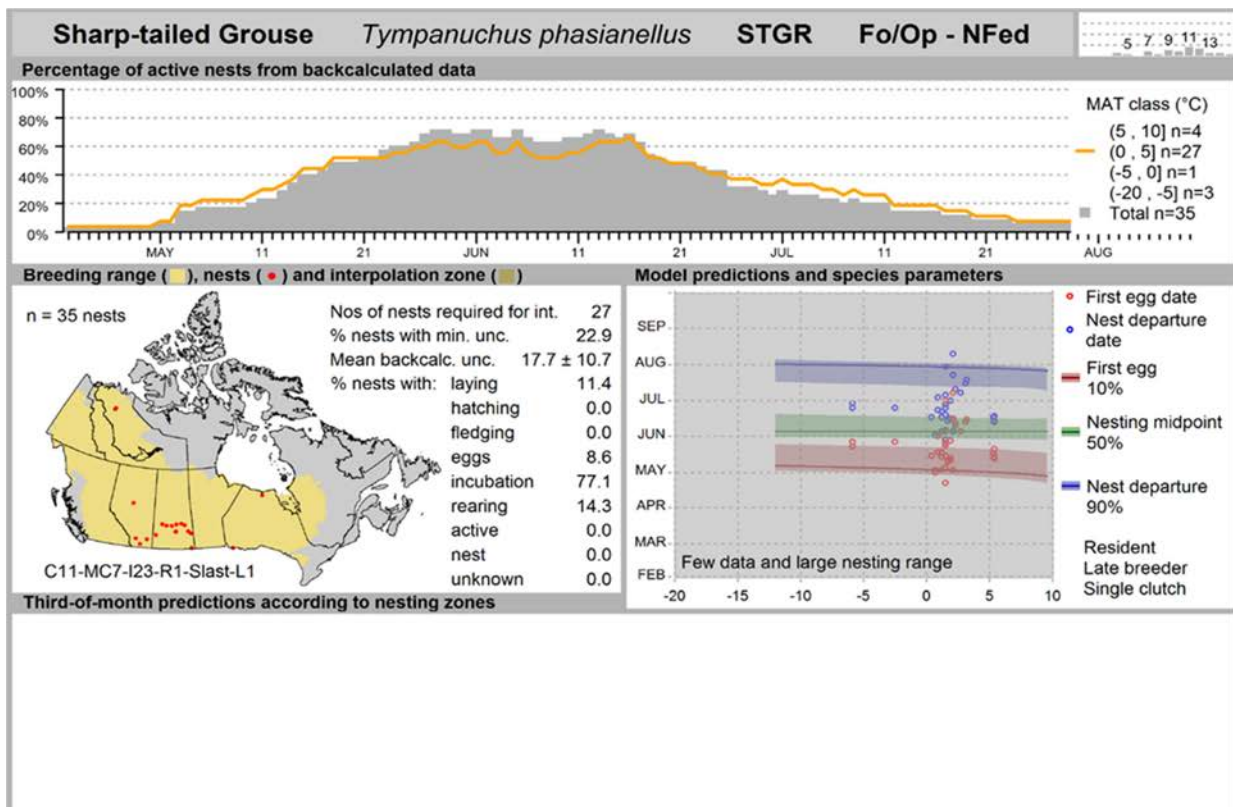


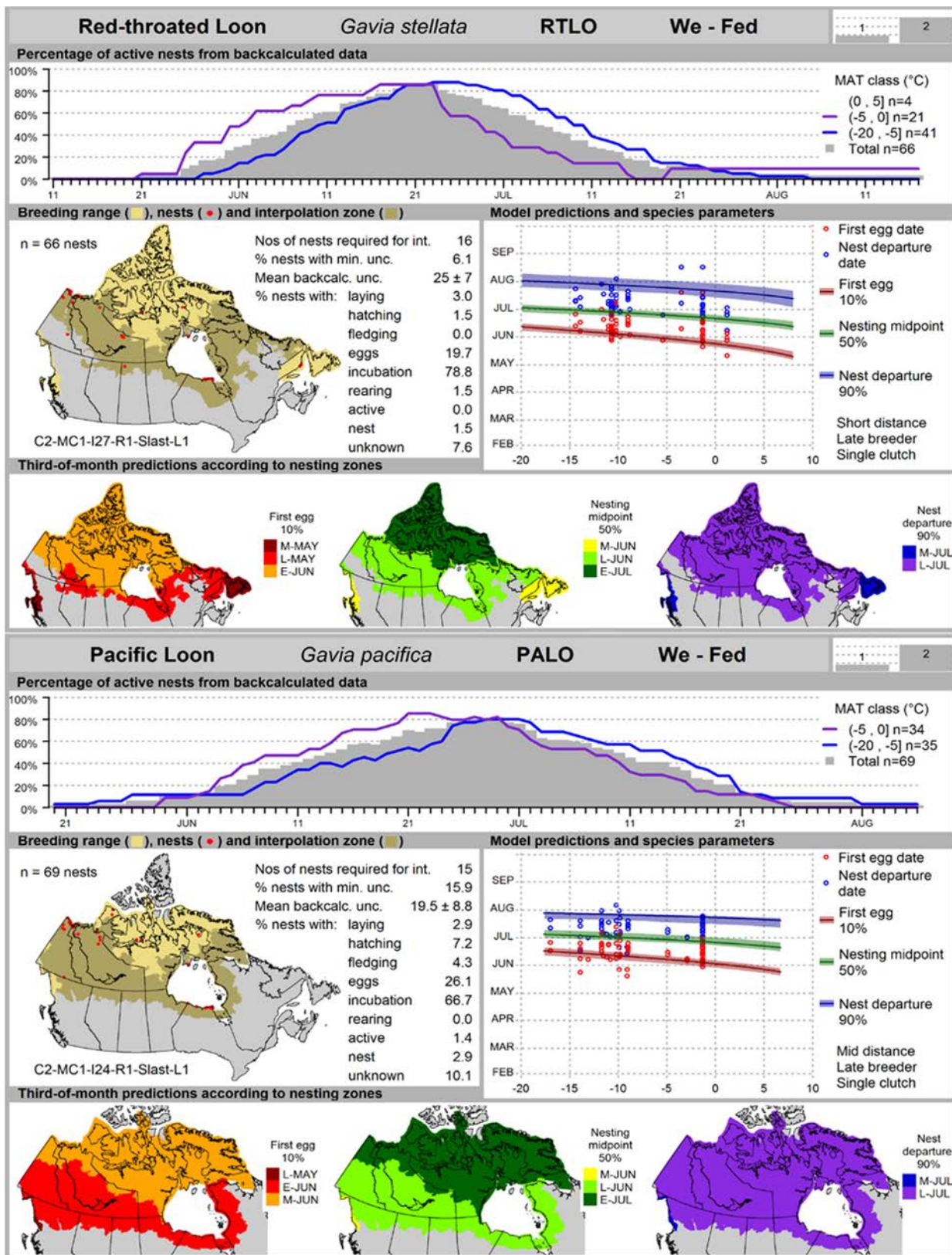


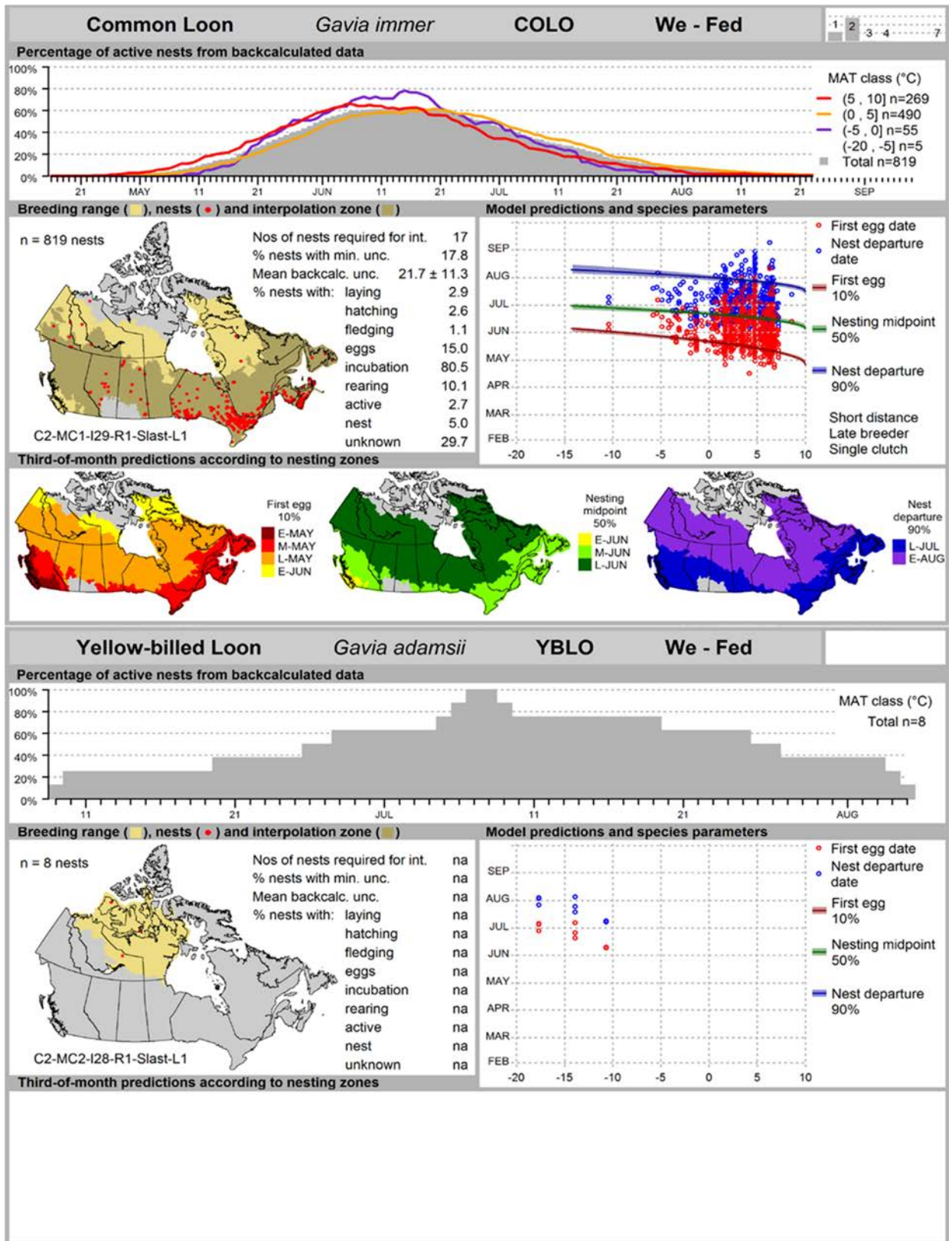


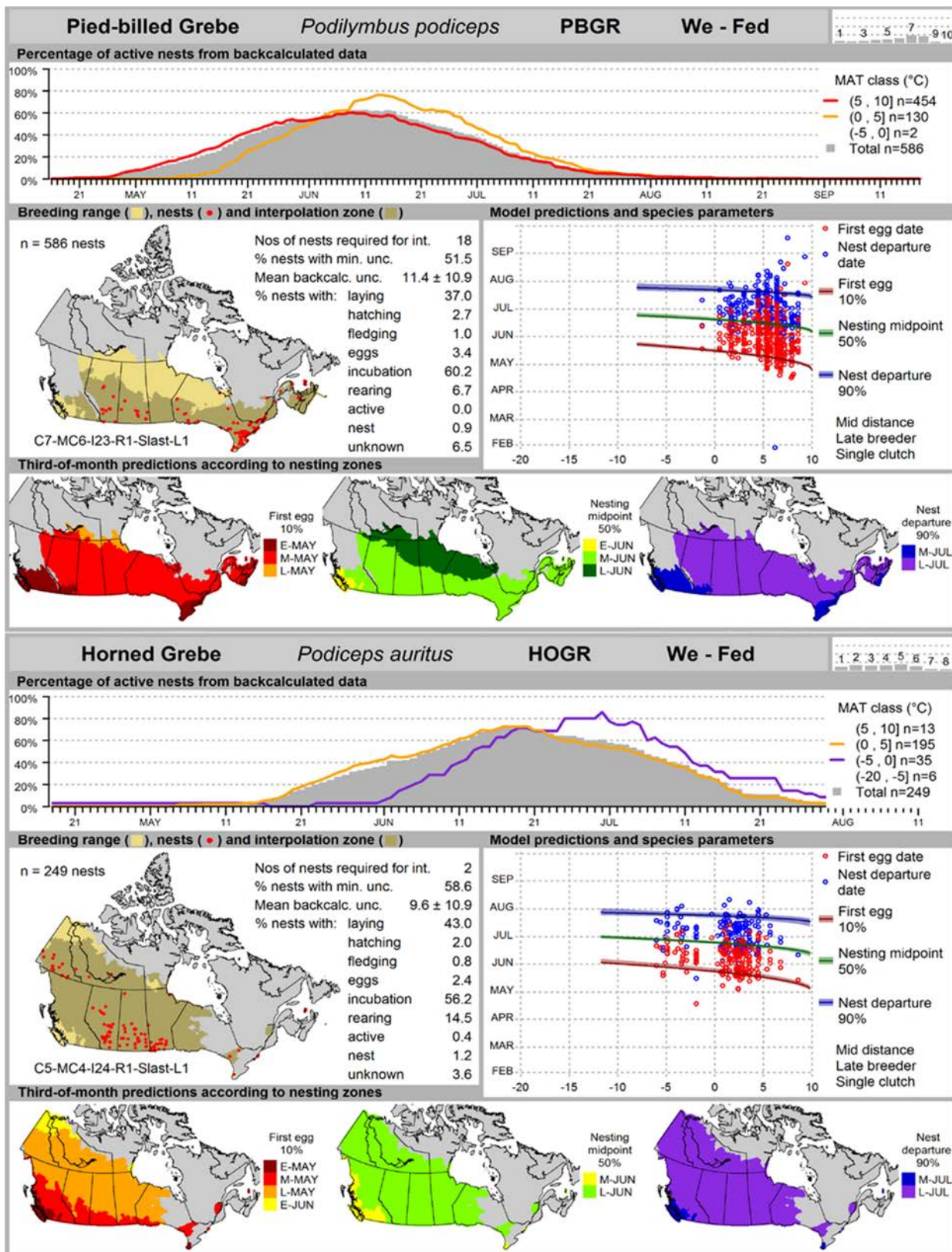


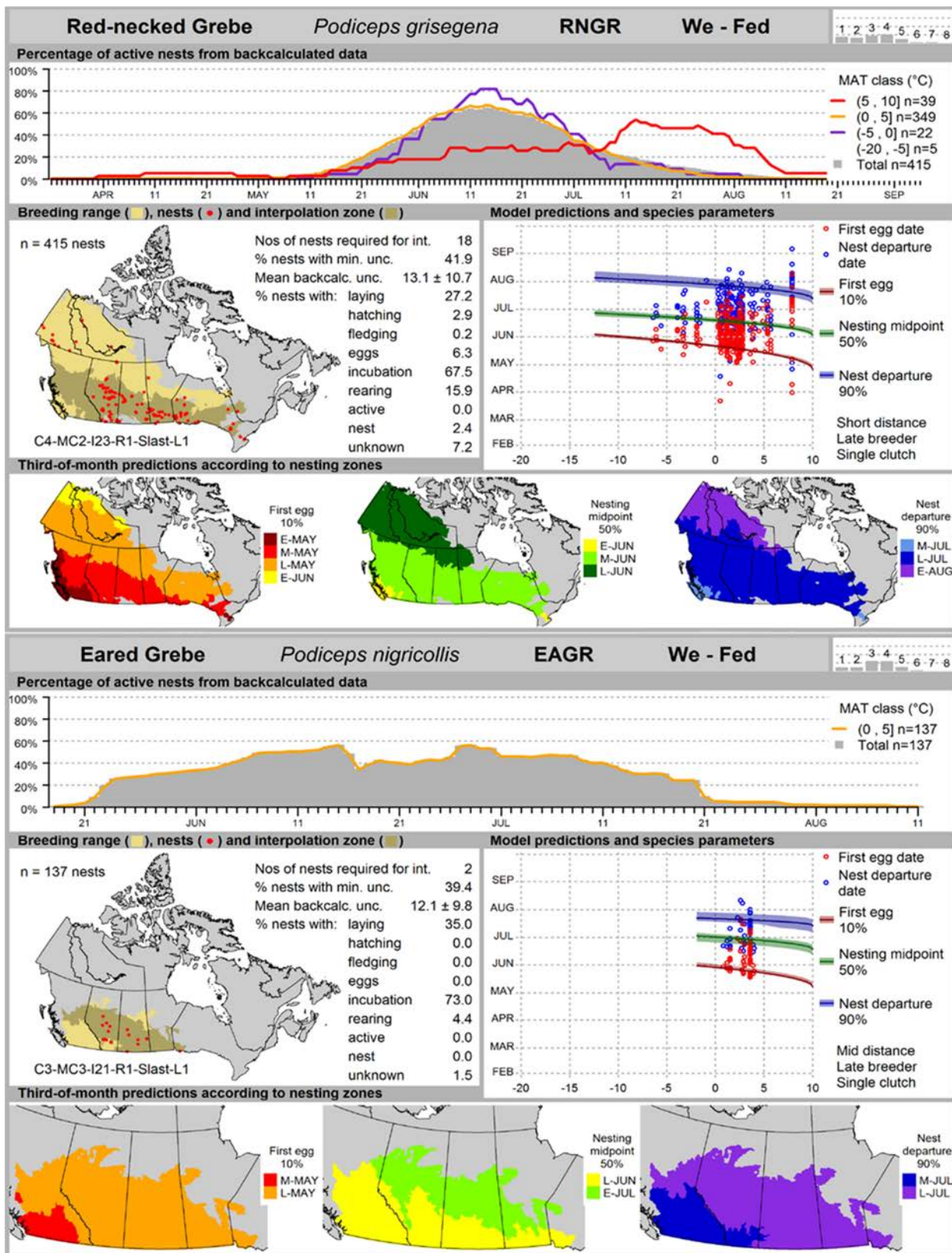


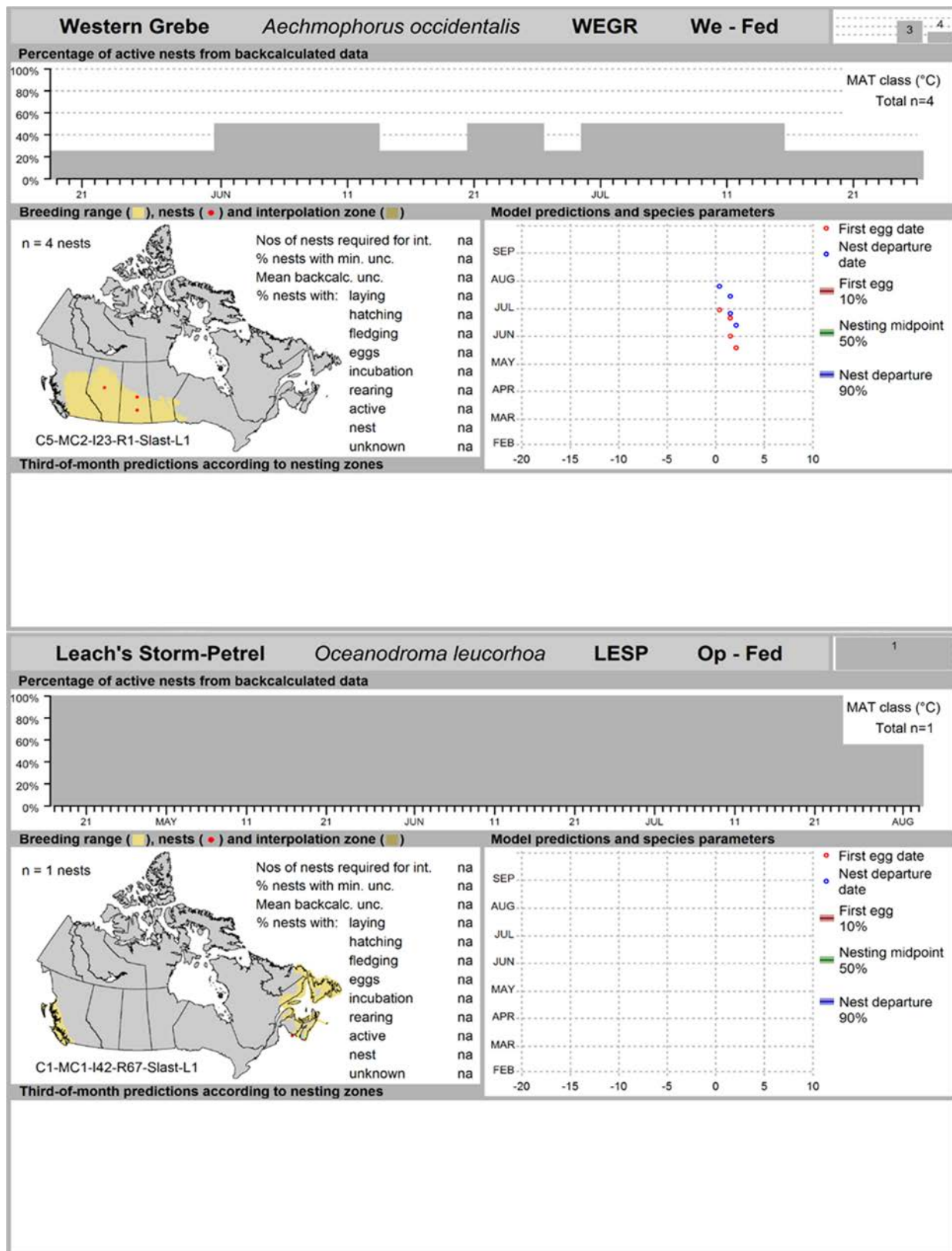


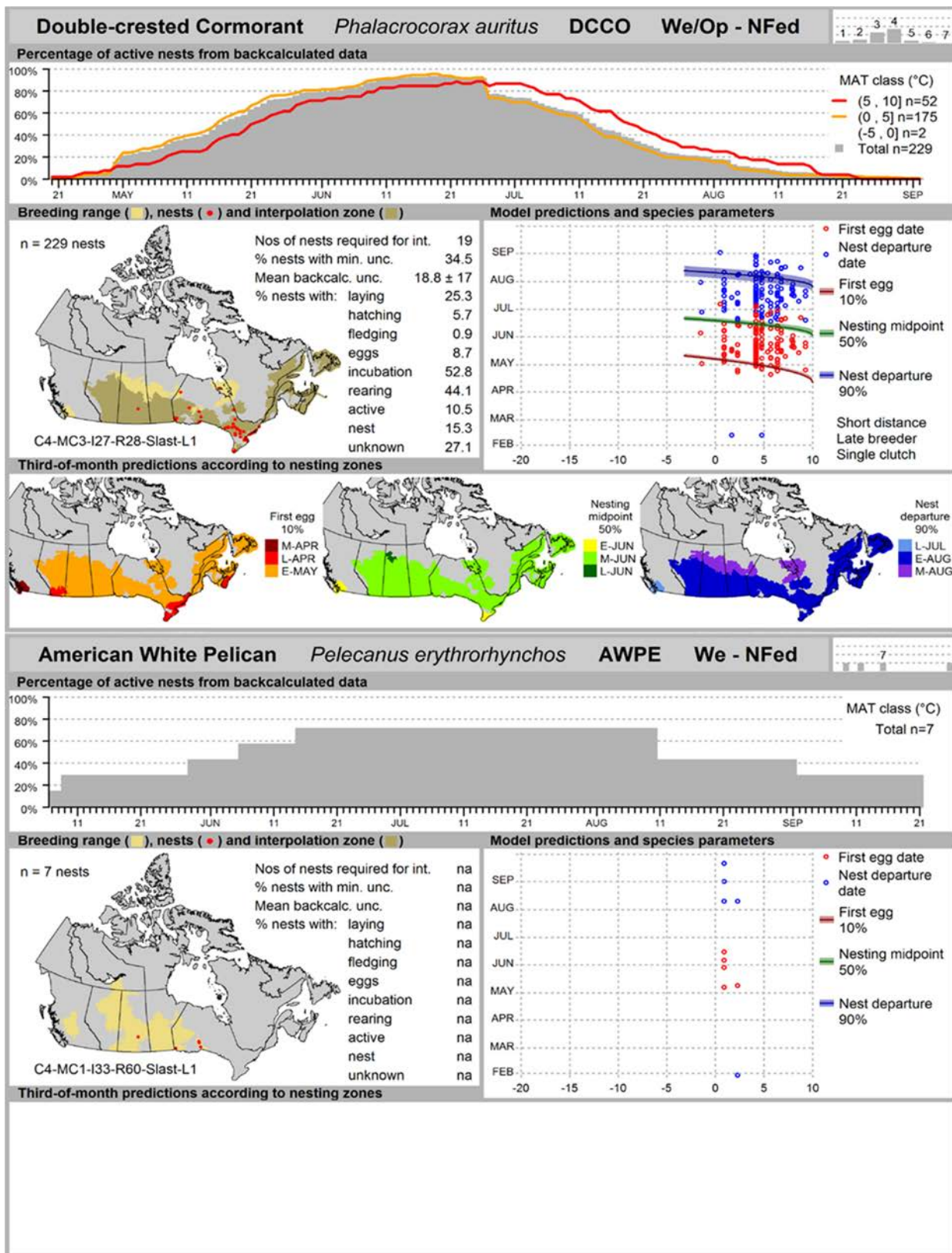












American White Pelican *Pelecanus erythrorhynchos* AWPE We - NFed

Percentage of active nests from backcalculated data

MAT class (°C)

Total n=7

Breeding range (), nests (•) and interpolation zone ()

n = 7 nests

Nos of nests required for int. na

% nests with min. unc. na

Mean backcalc. unc. na

% nests with:

laying	na
hatching	na
fledging	na
eggs	na
incubation	na
rearing	na
active	na
nest	na
unknown	na

C4-MC1-I33-R60-Slast-L1

Model predictions and species parameters

First egg date

Nest departure date

First egg 10%

Nesting midpoint 50%

Nest departure 90%

Third-of-month predictions according to nesting zones

First egg 10%

M-APR

L-APR

E-MAY

Nesting midpoint 50%

E-JUN

M-JUN

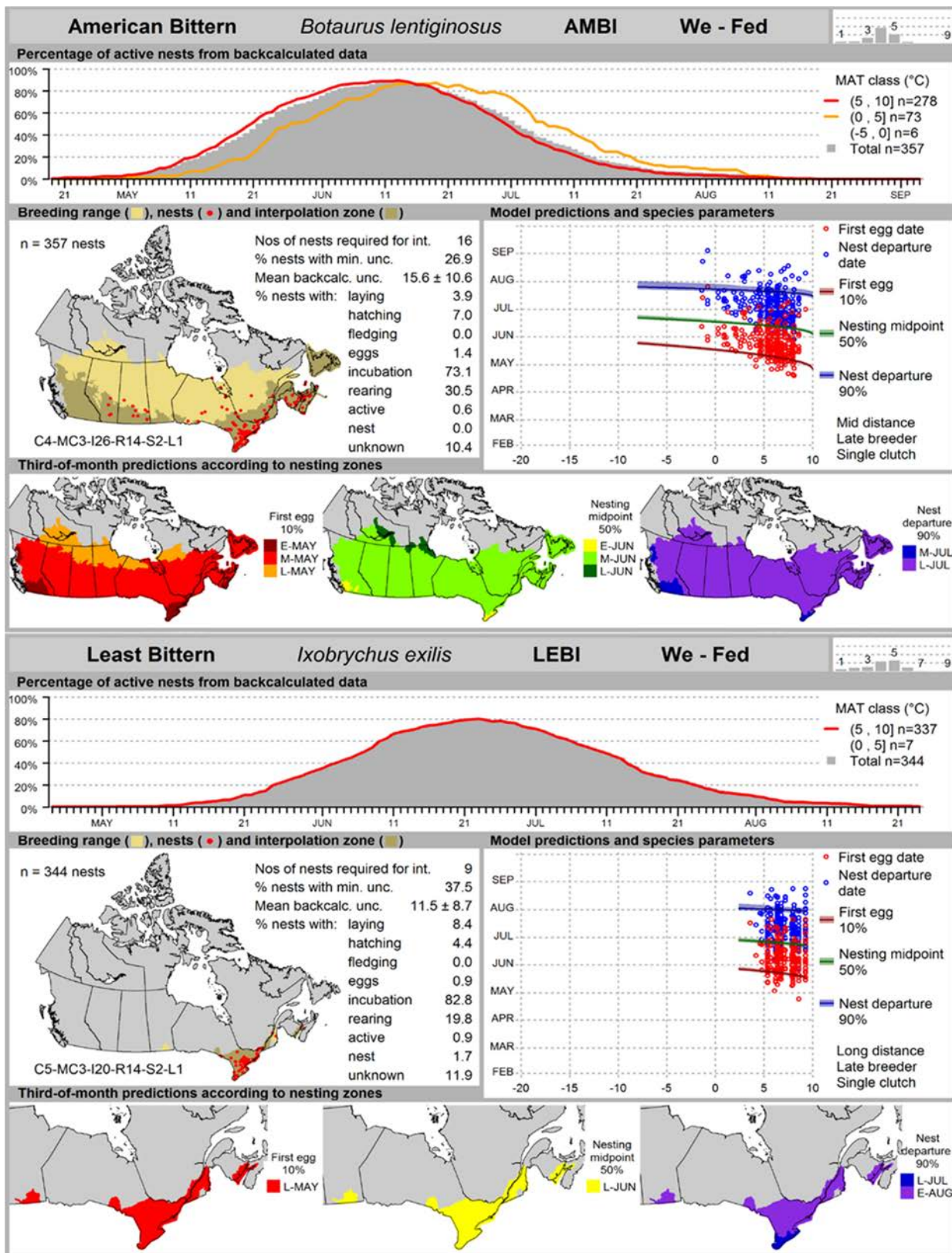
L-JUN

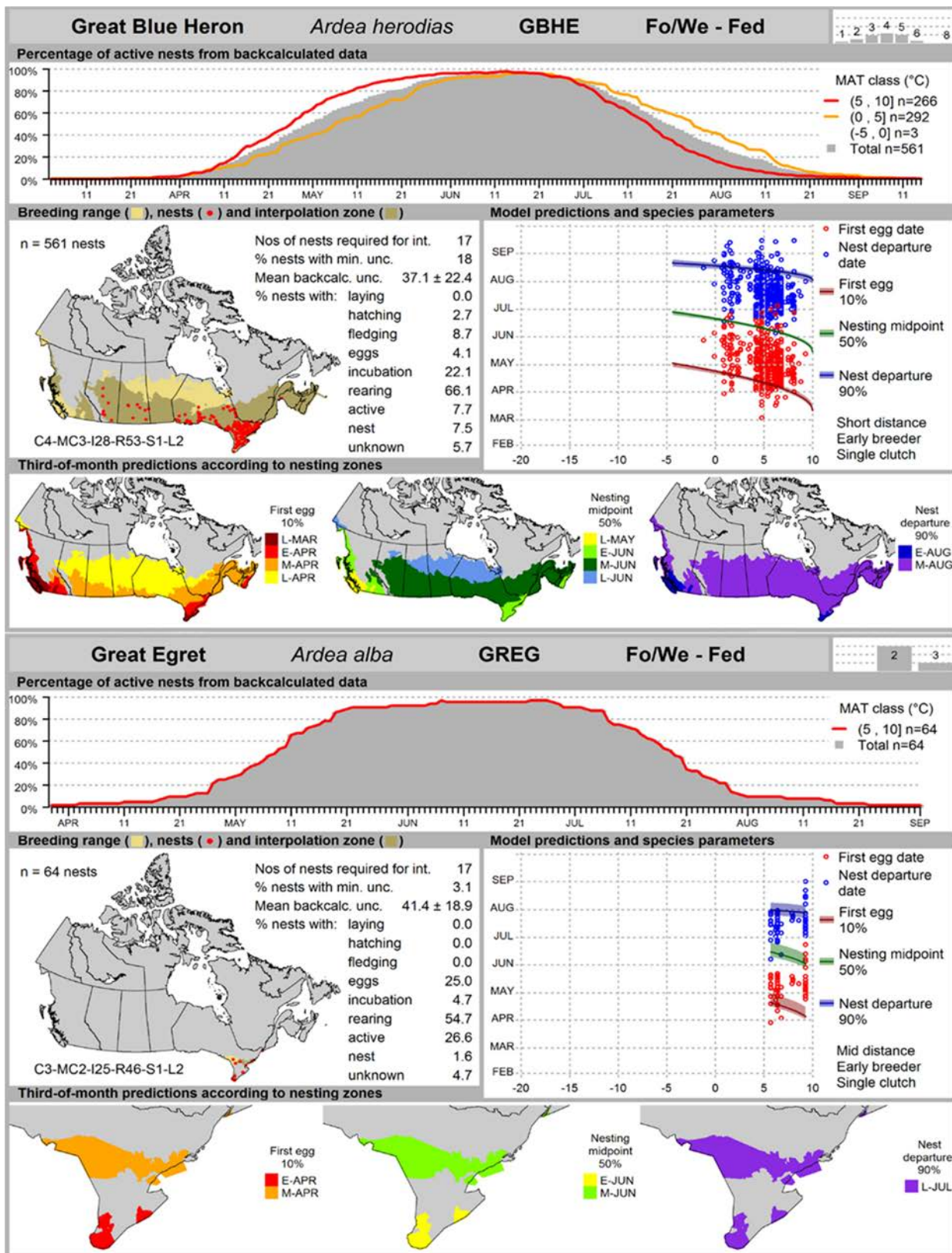
Nest departure 90%

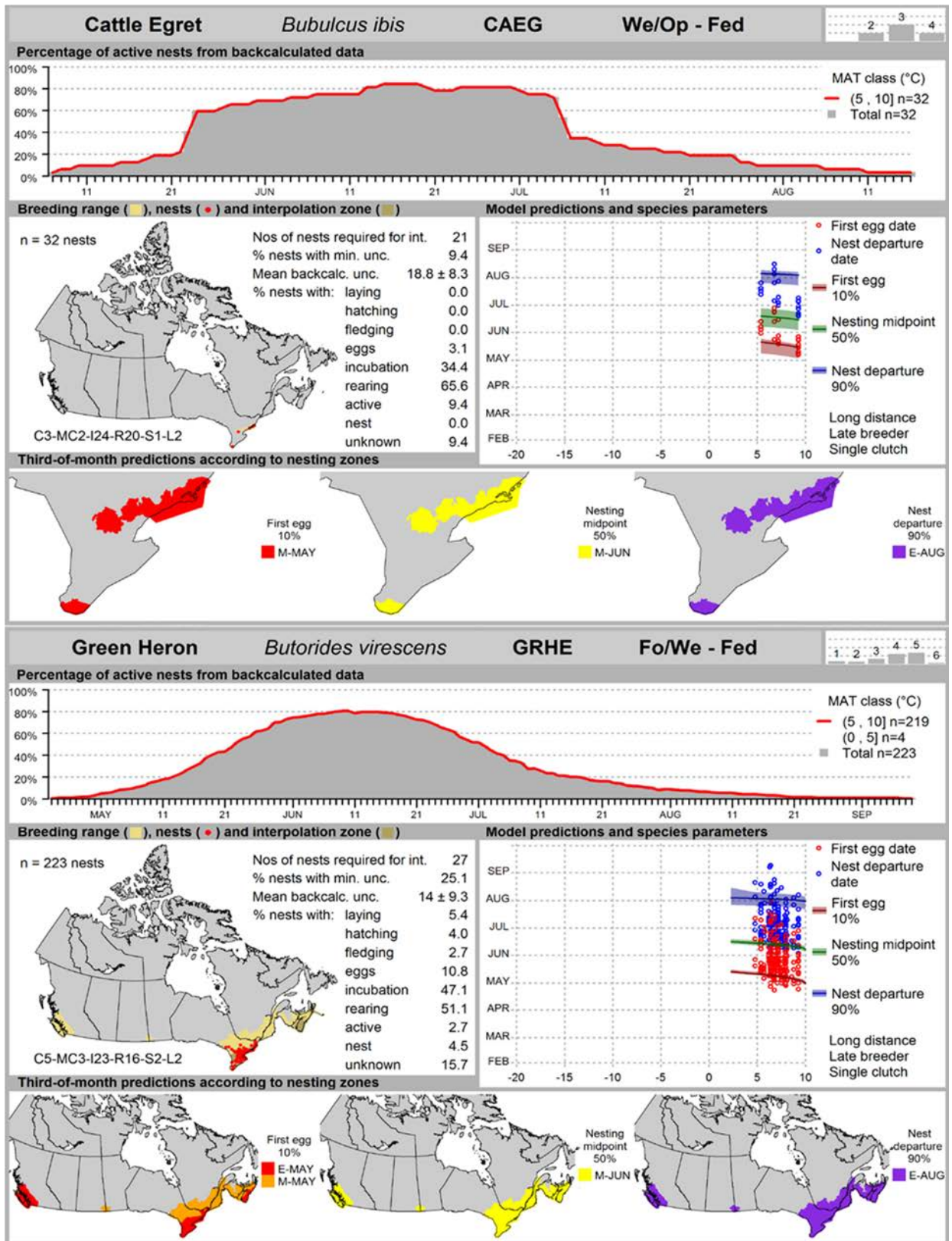
L-JUL

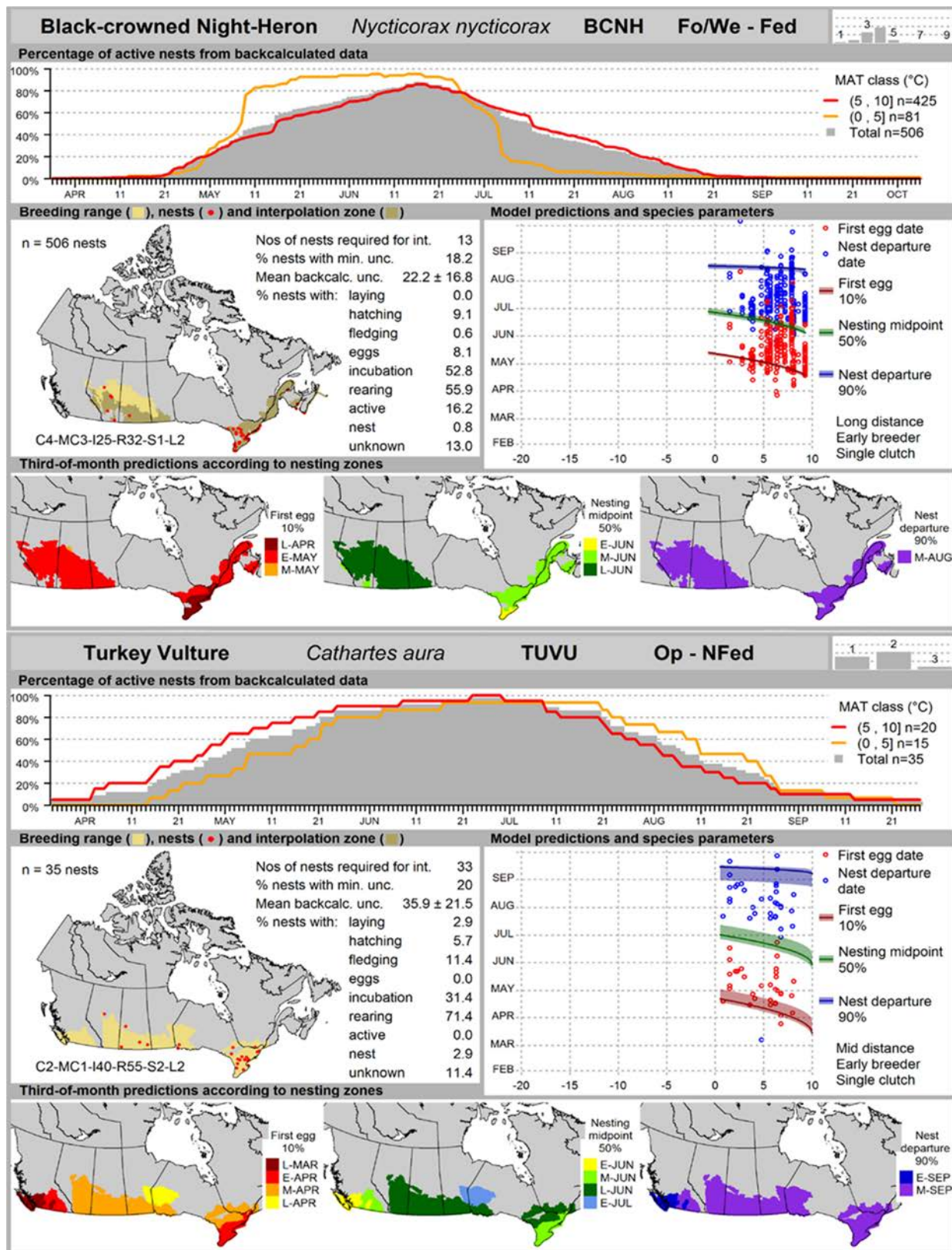
E-AUG

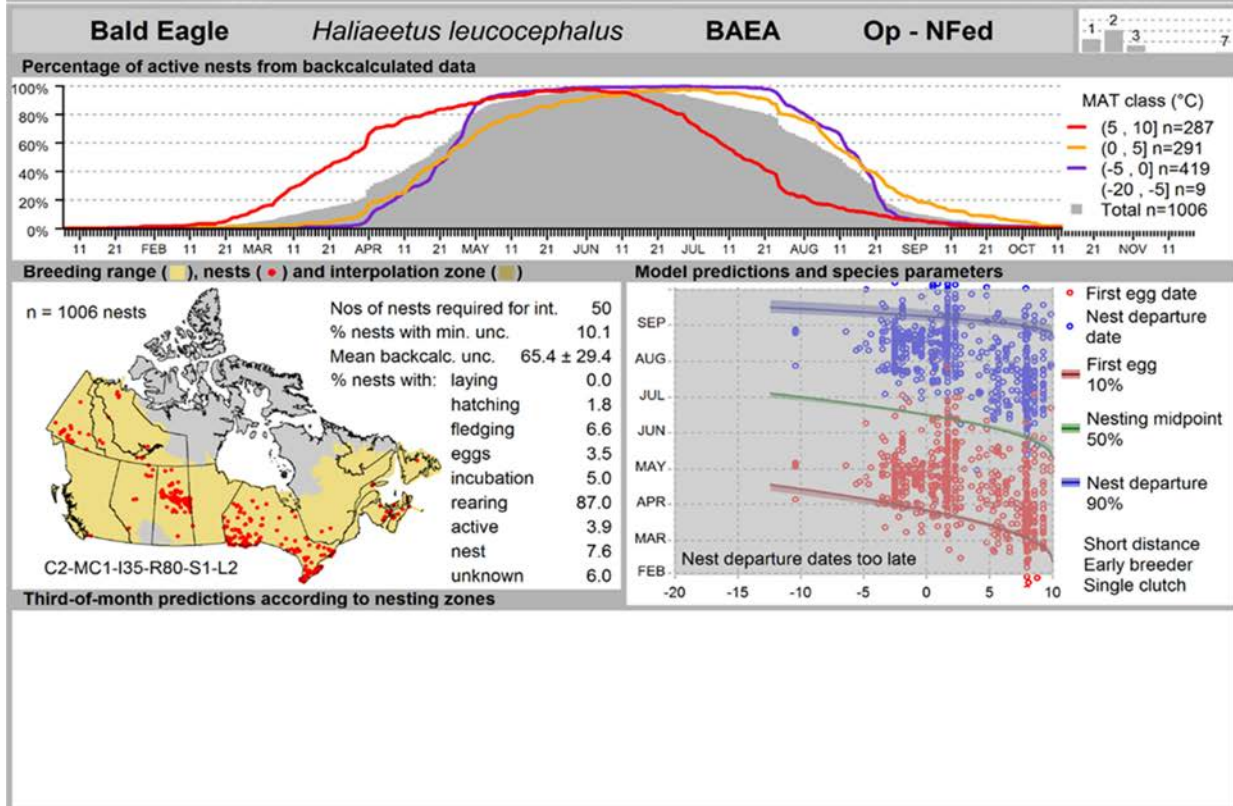
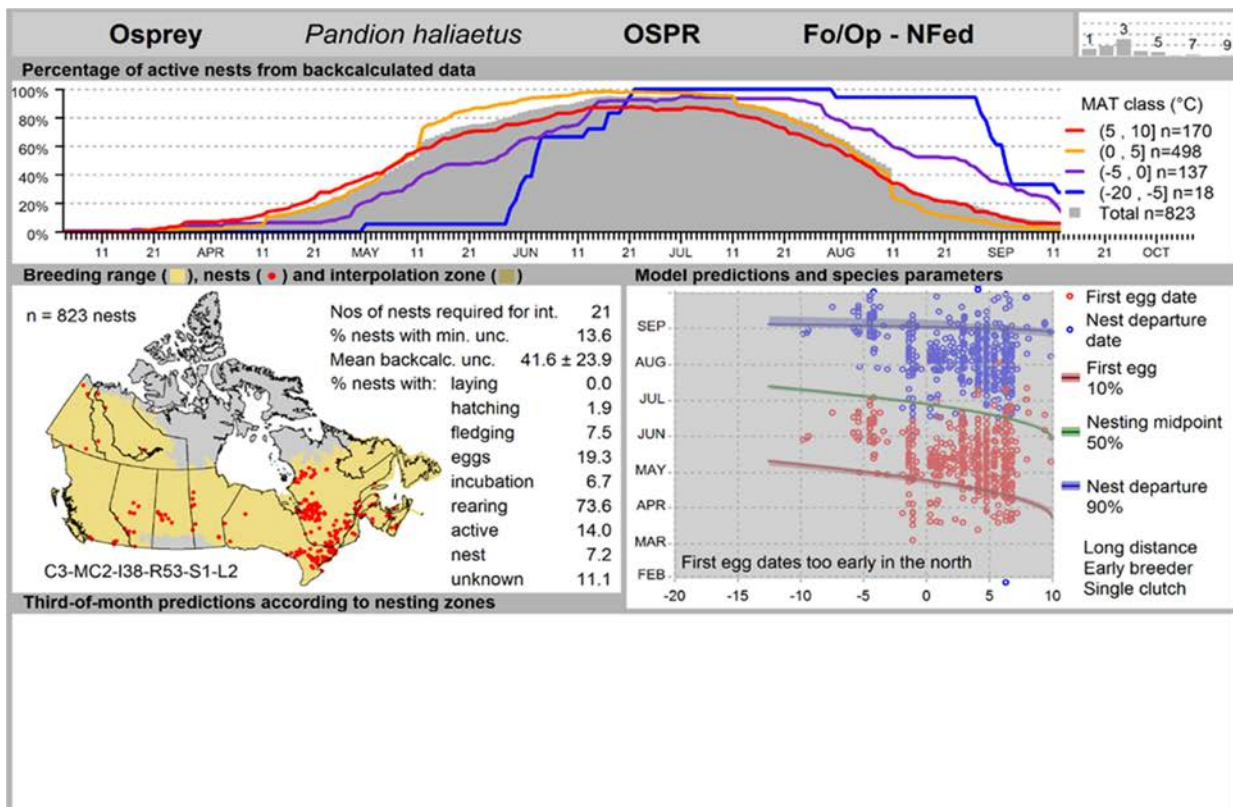
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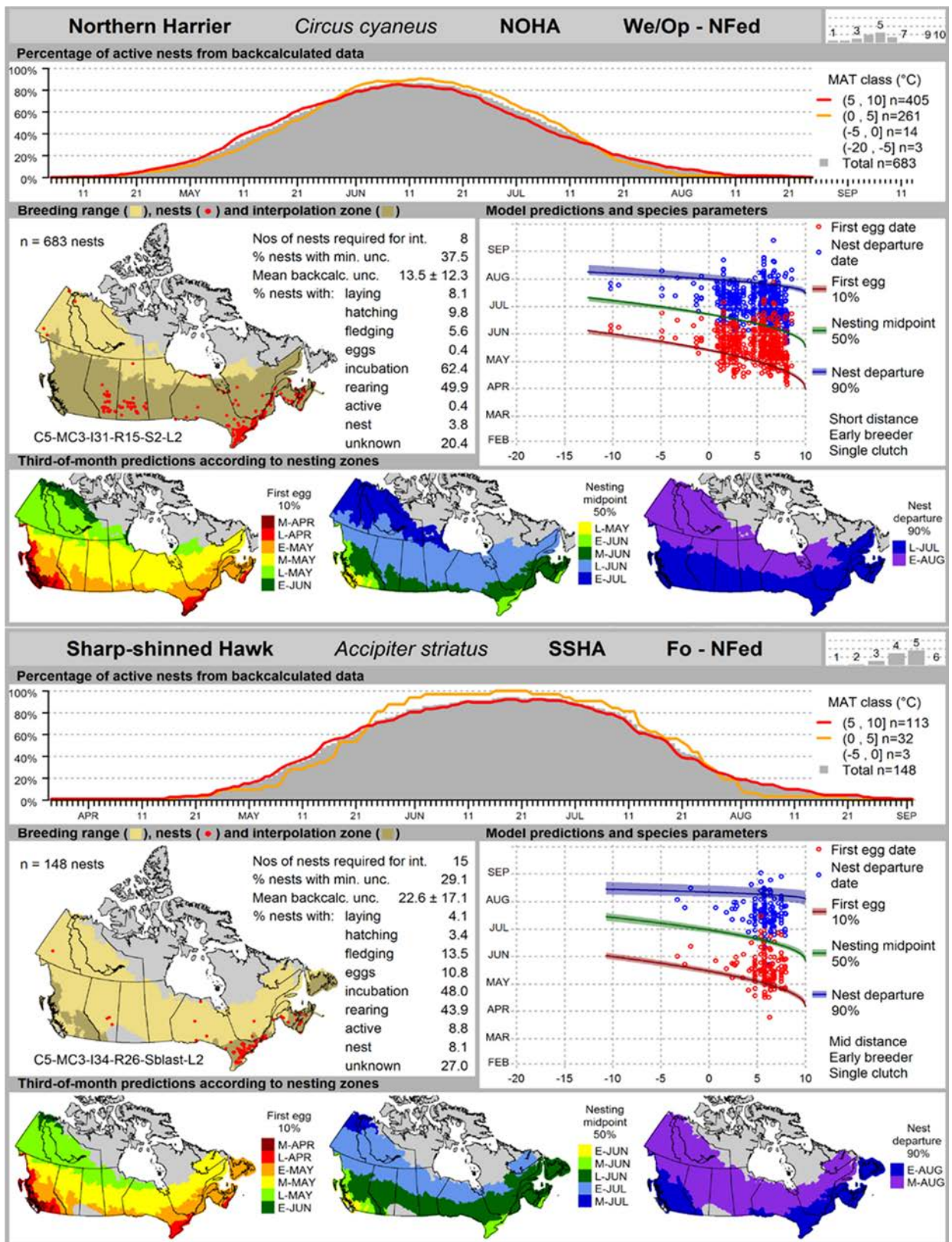


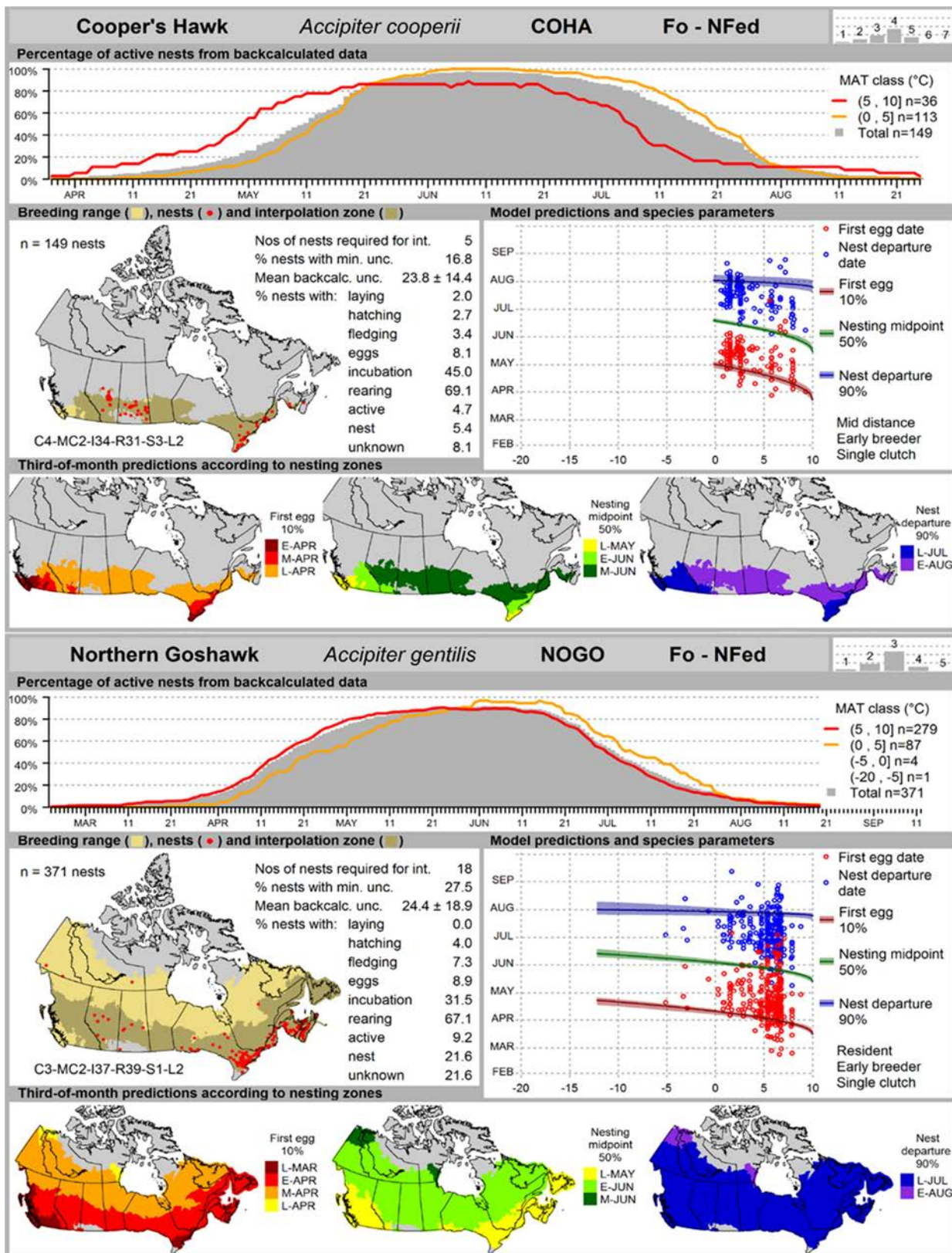


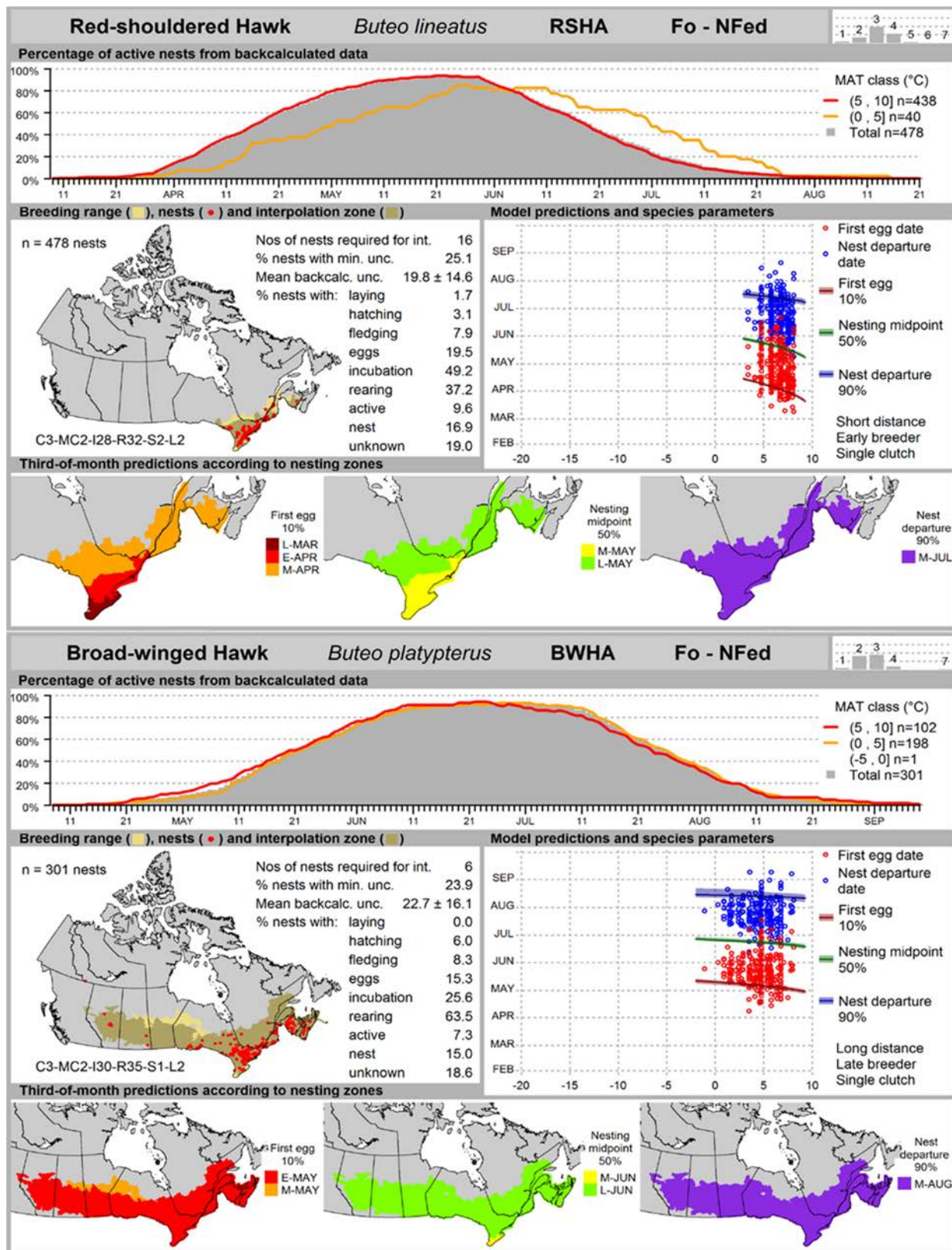


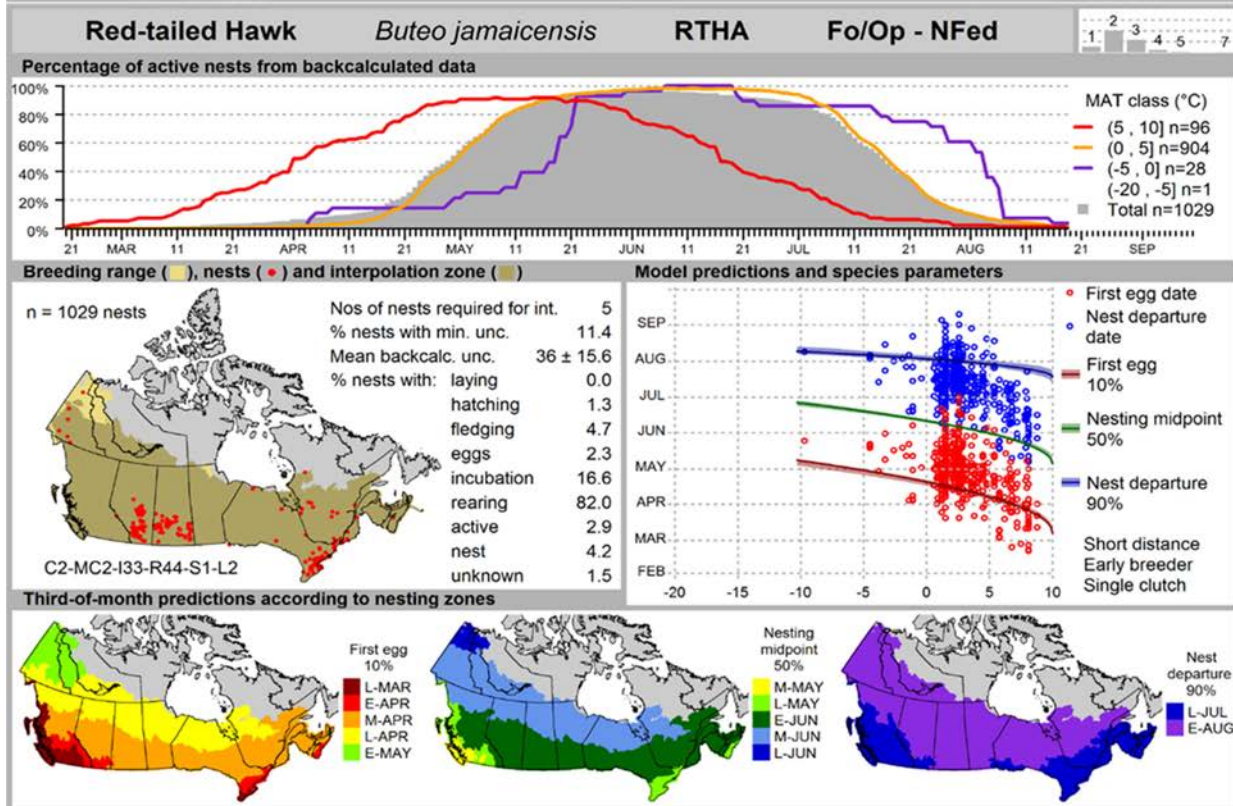
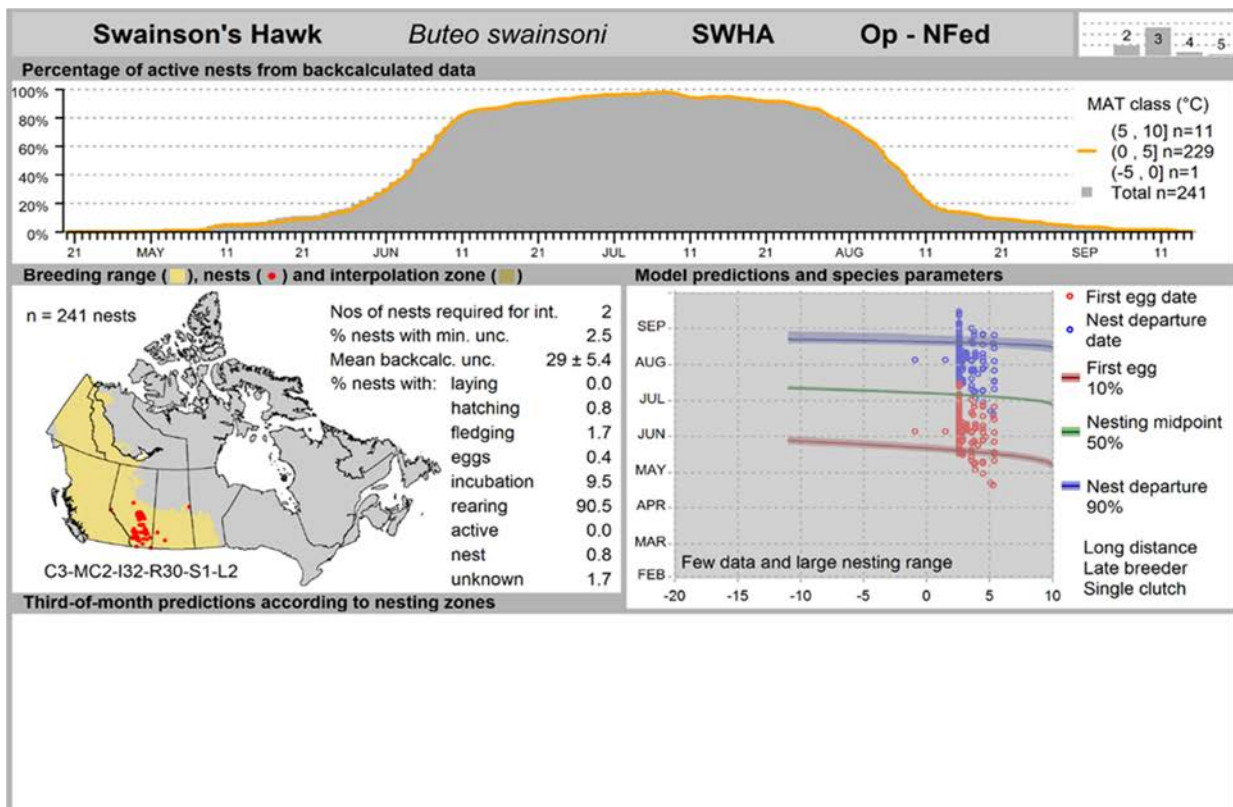


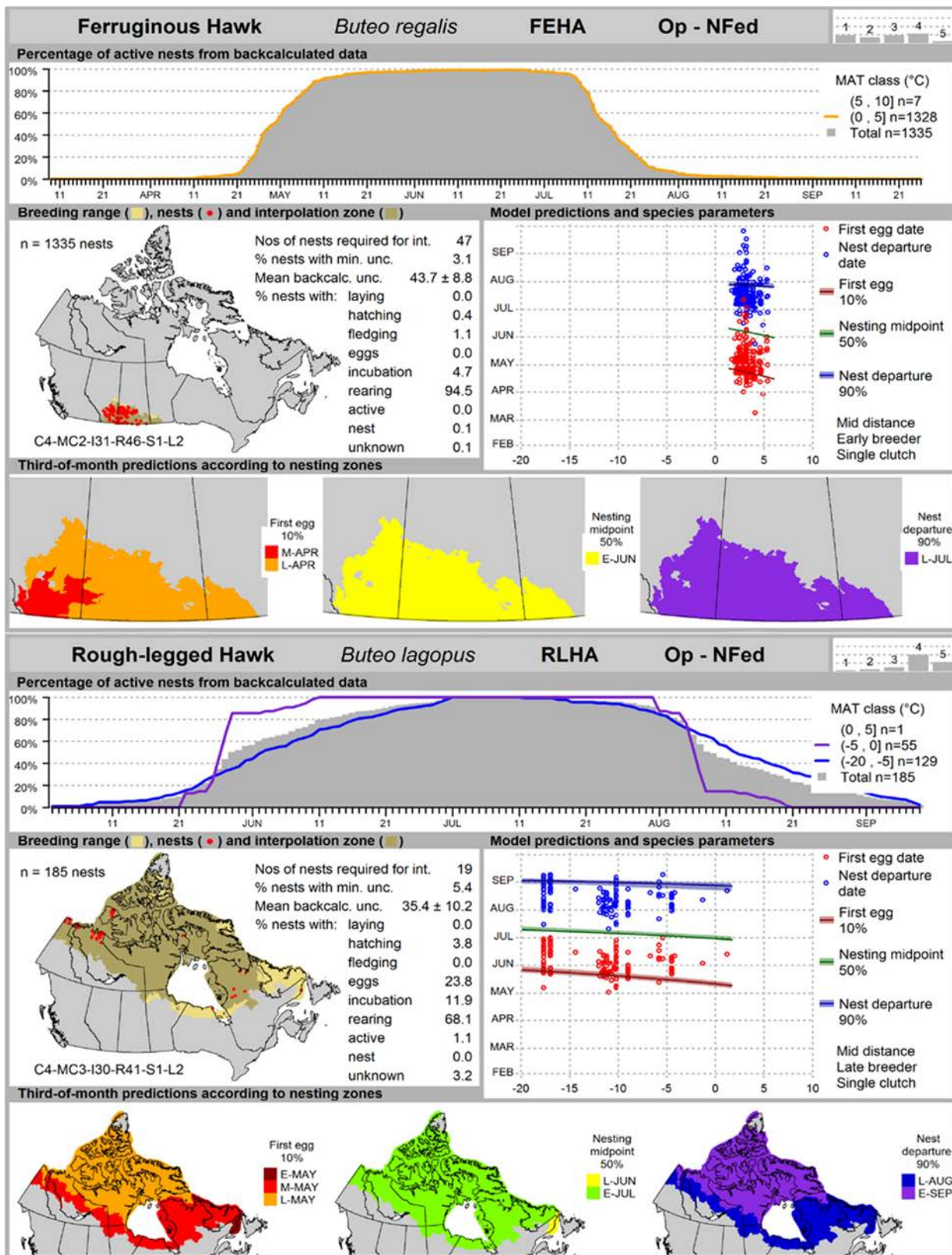


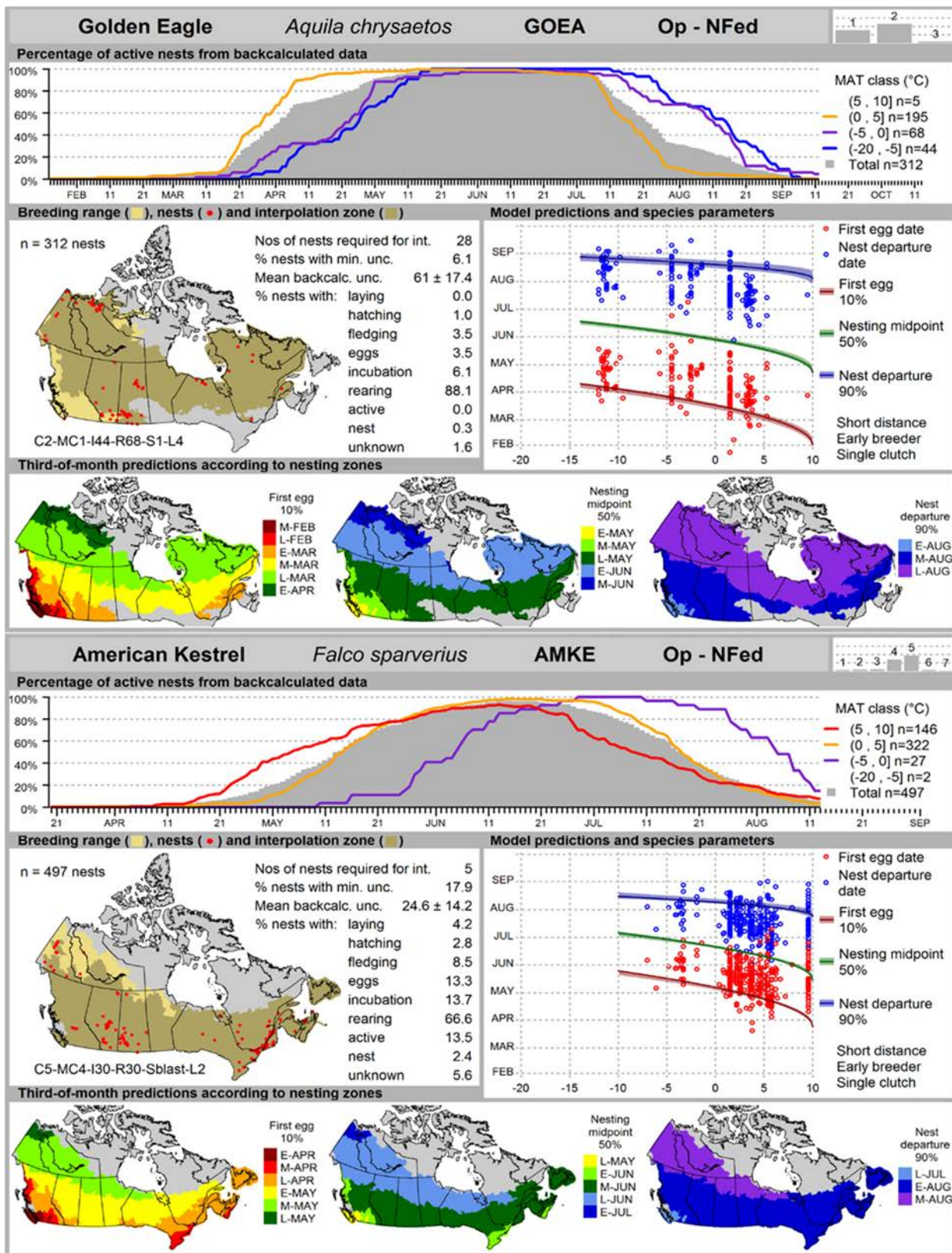


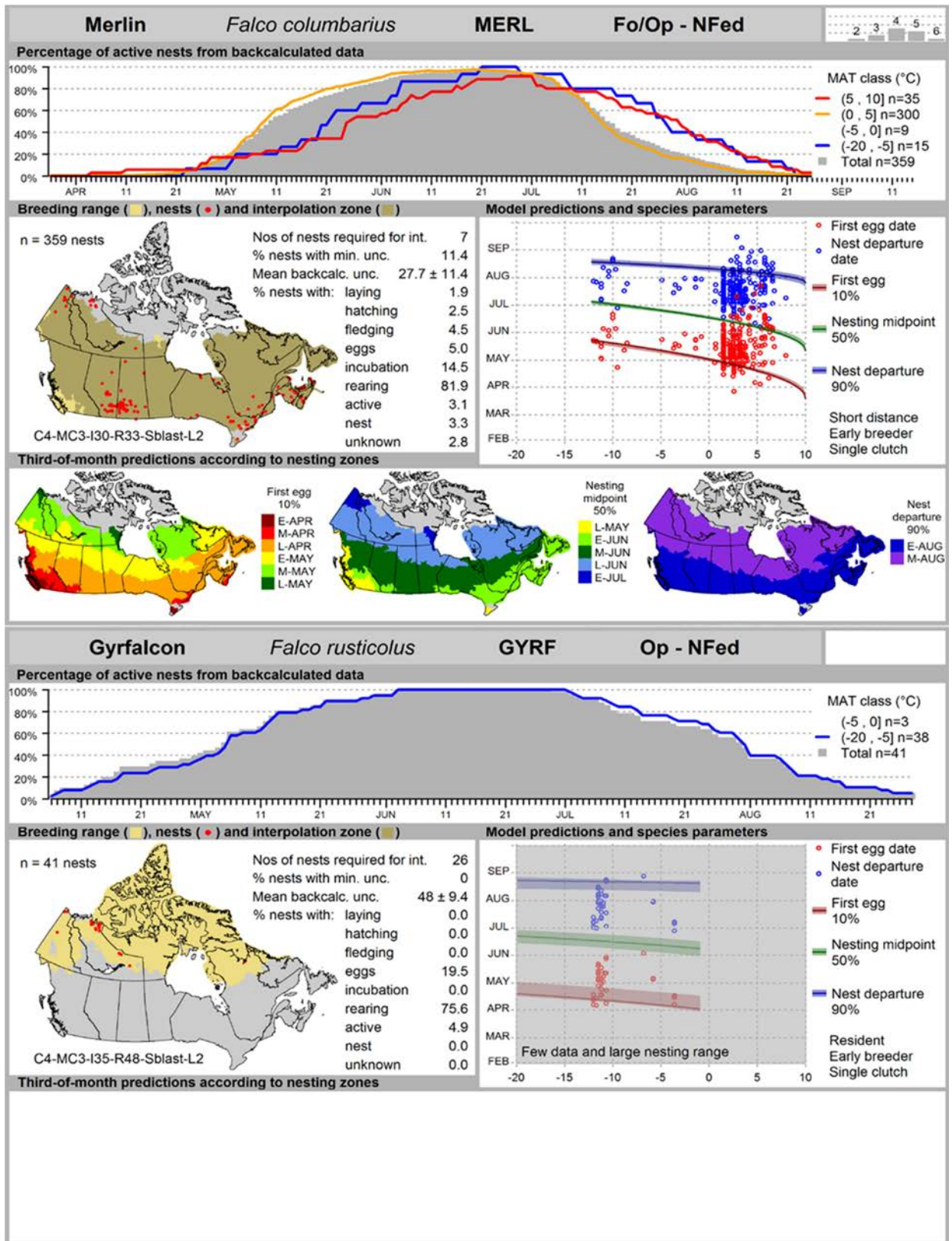


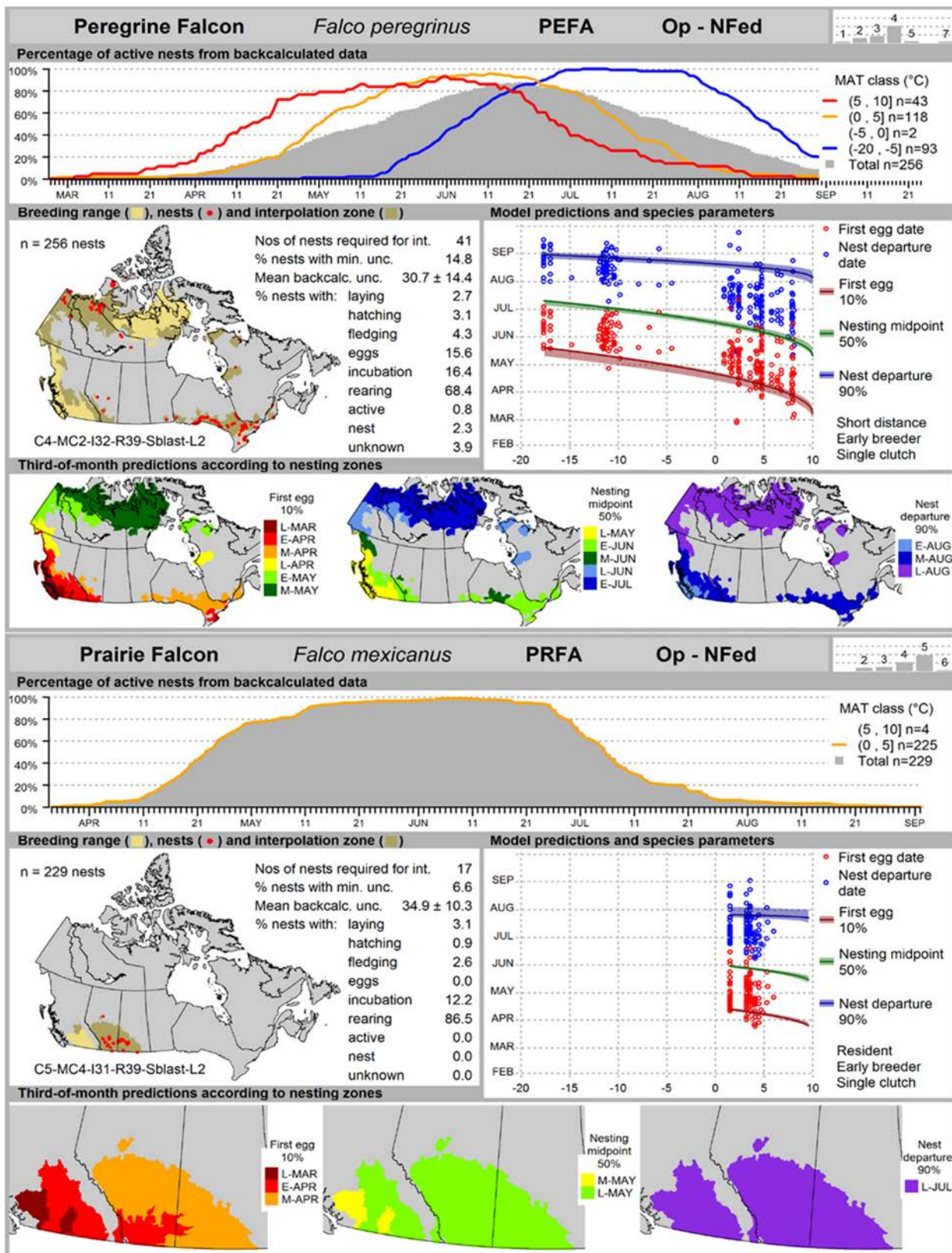


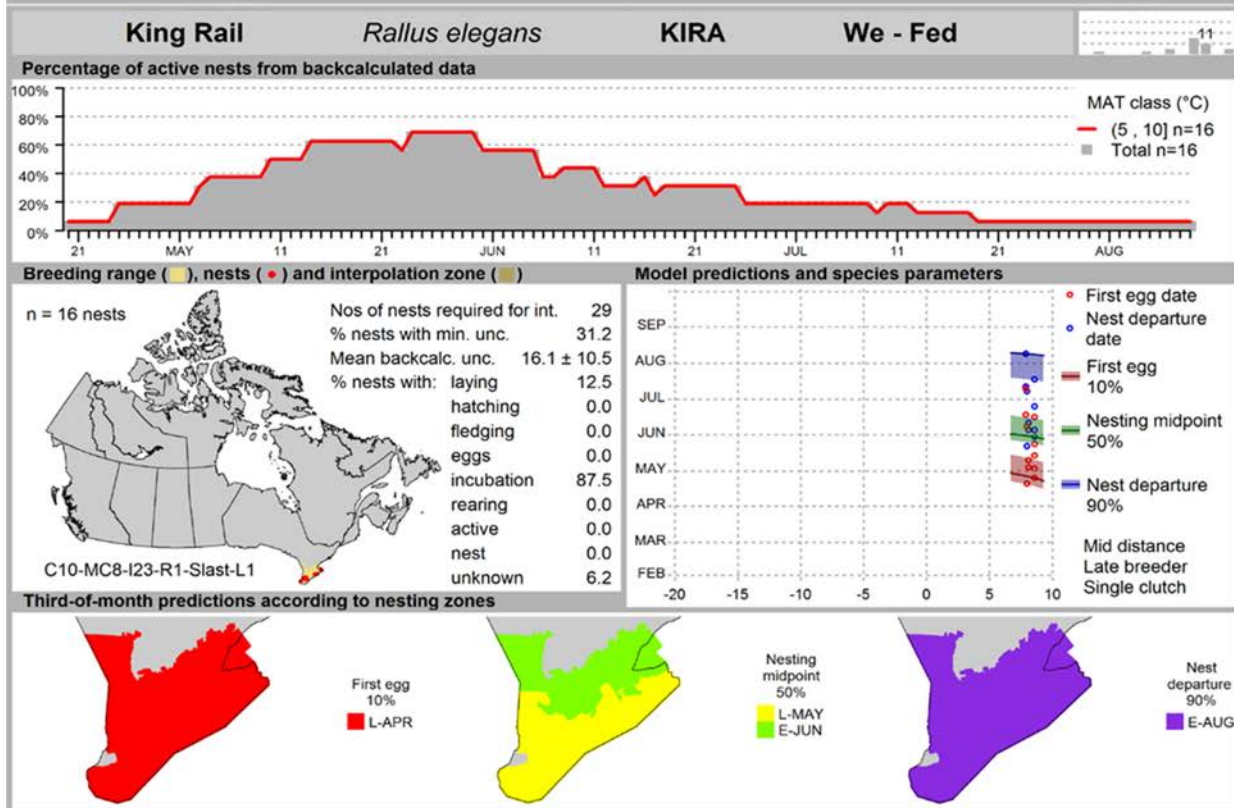
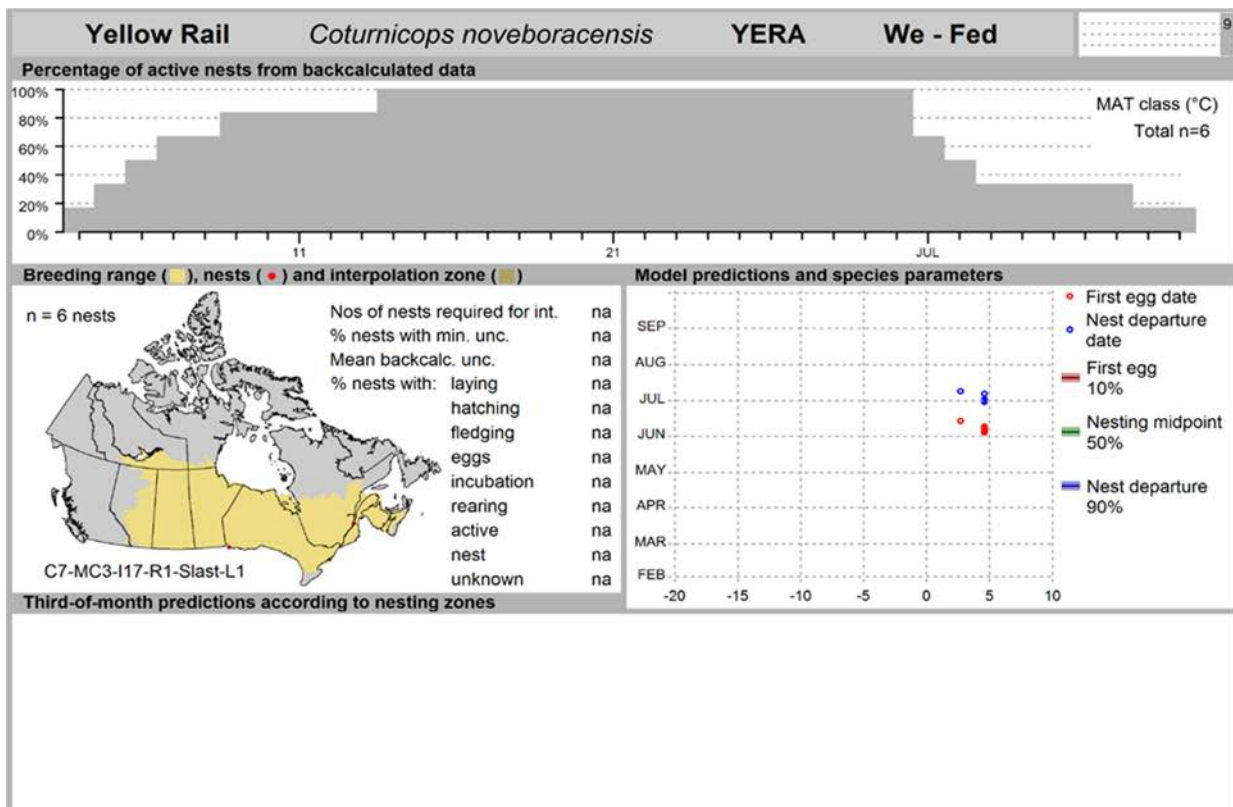


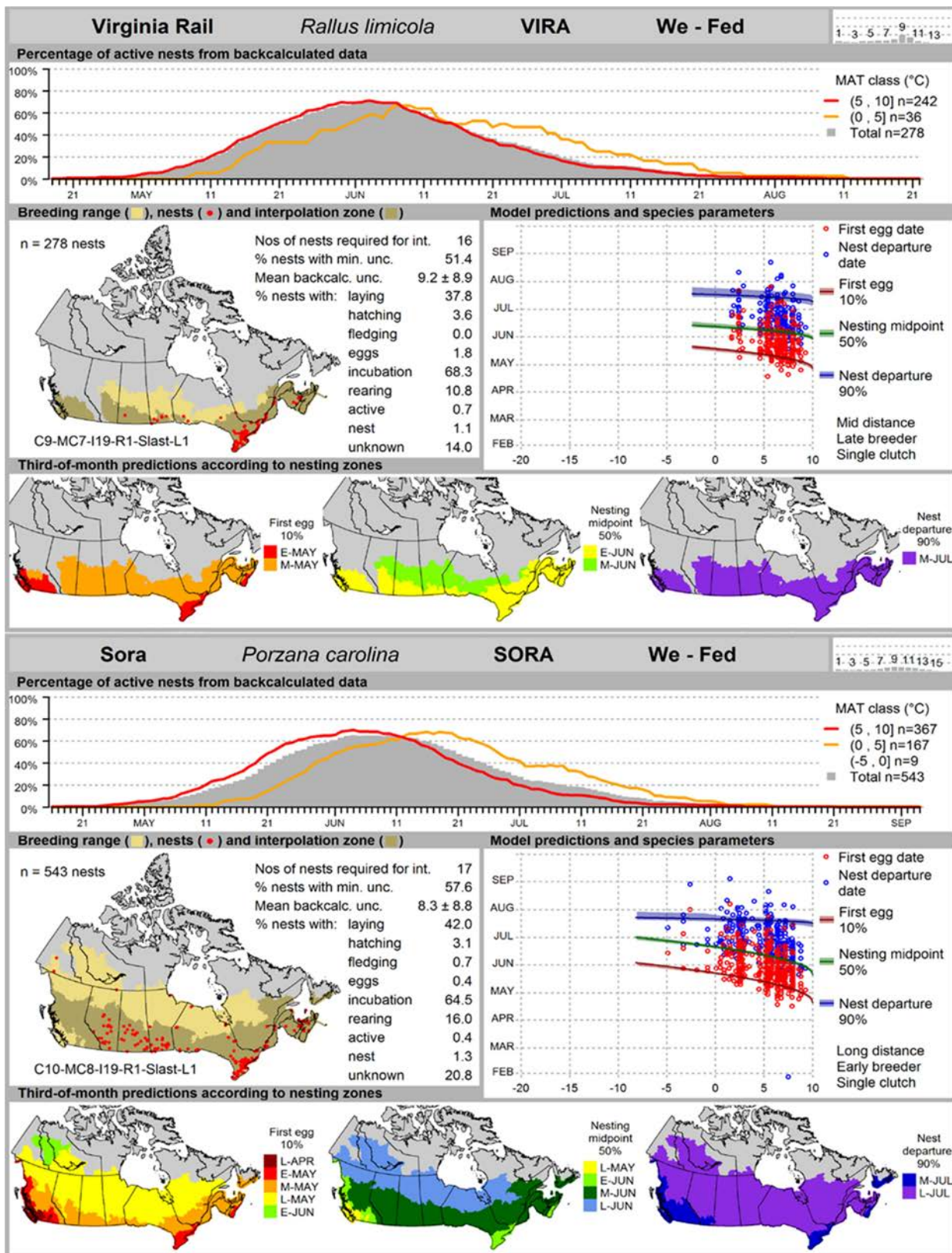


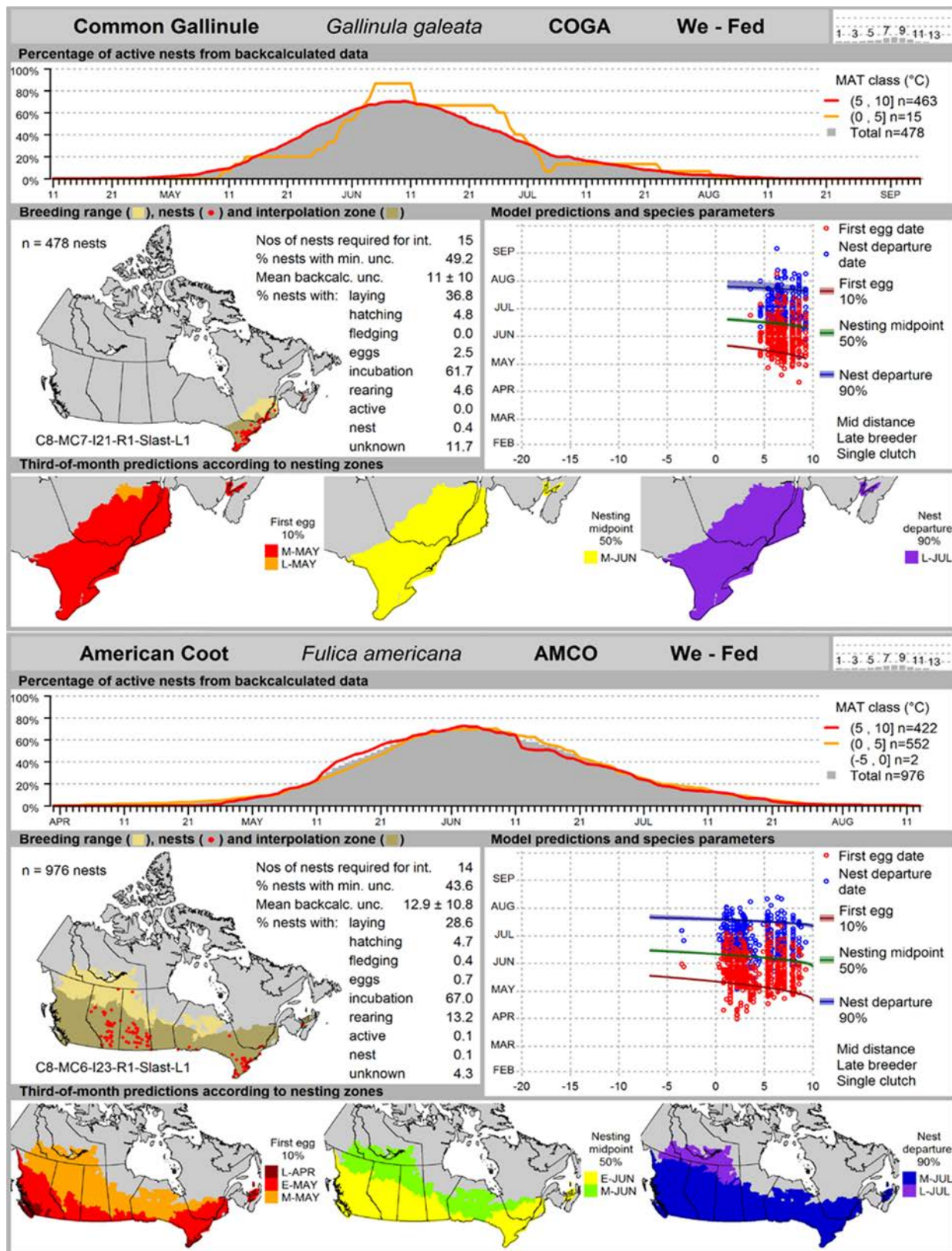


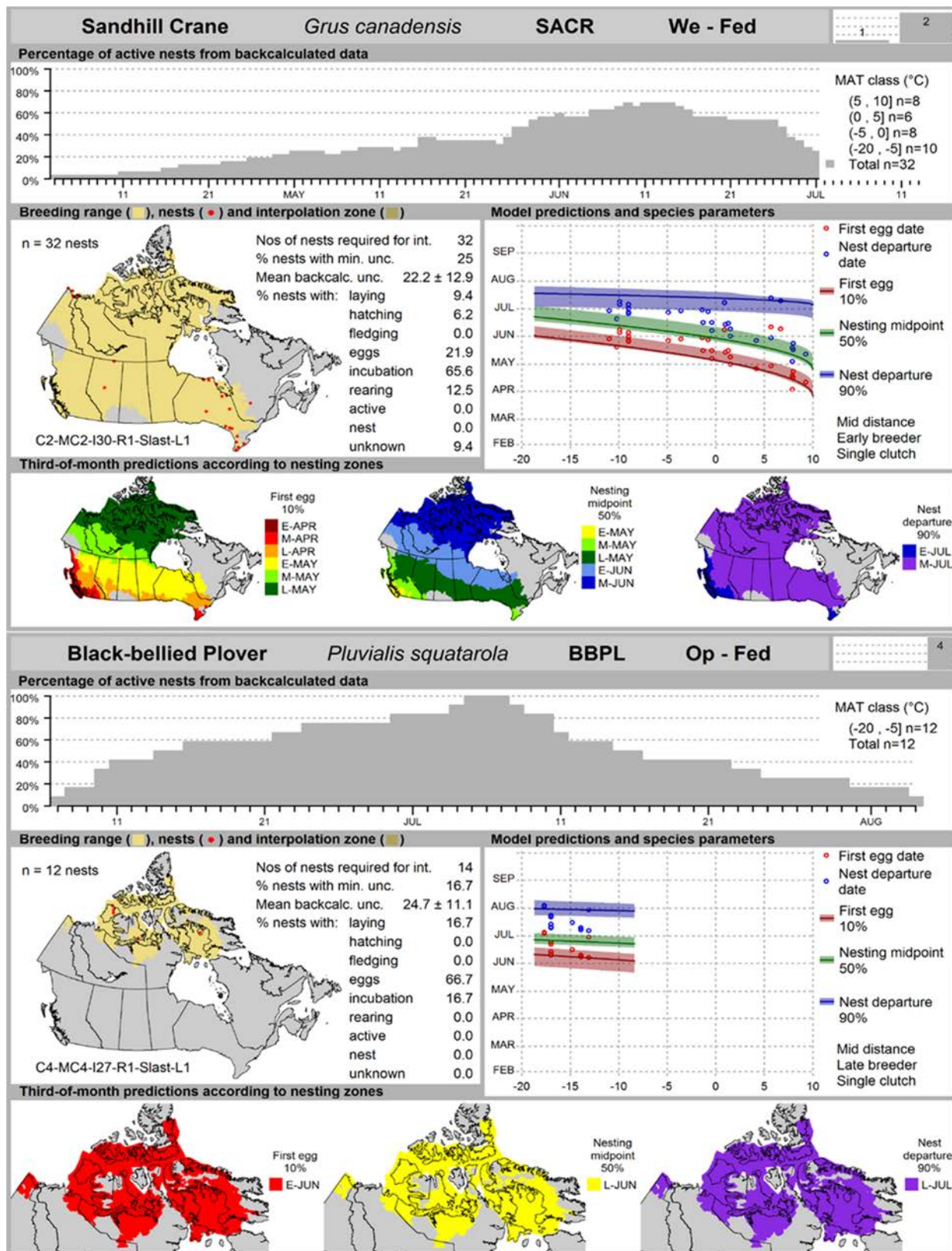


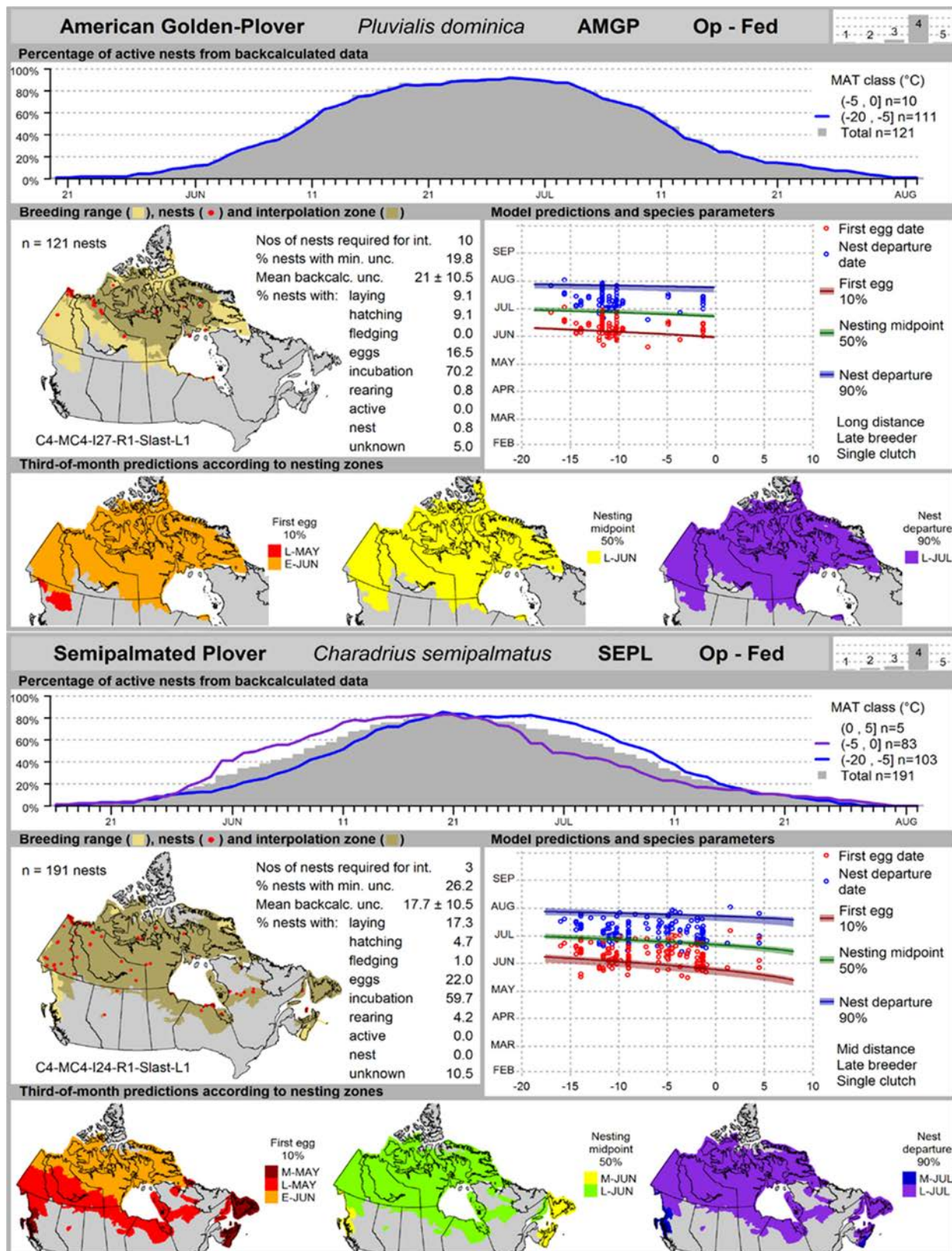


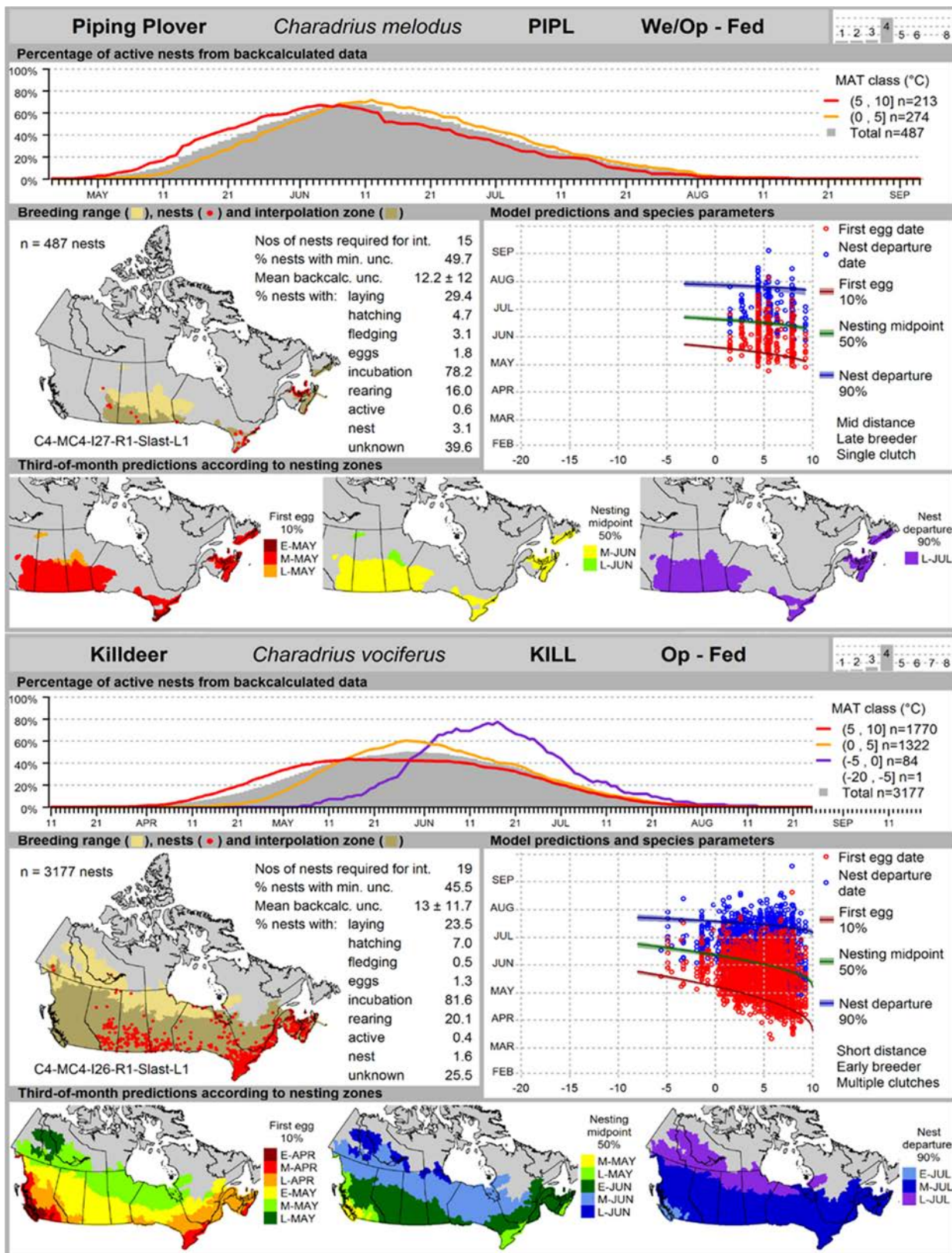


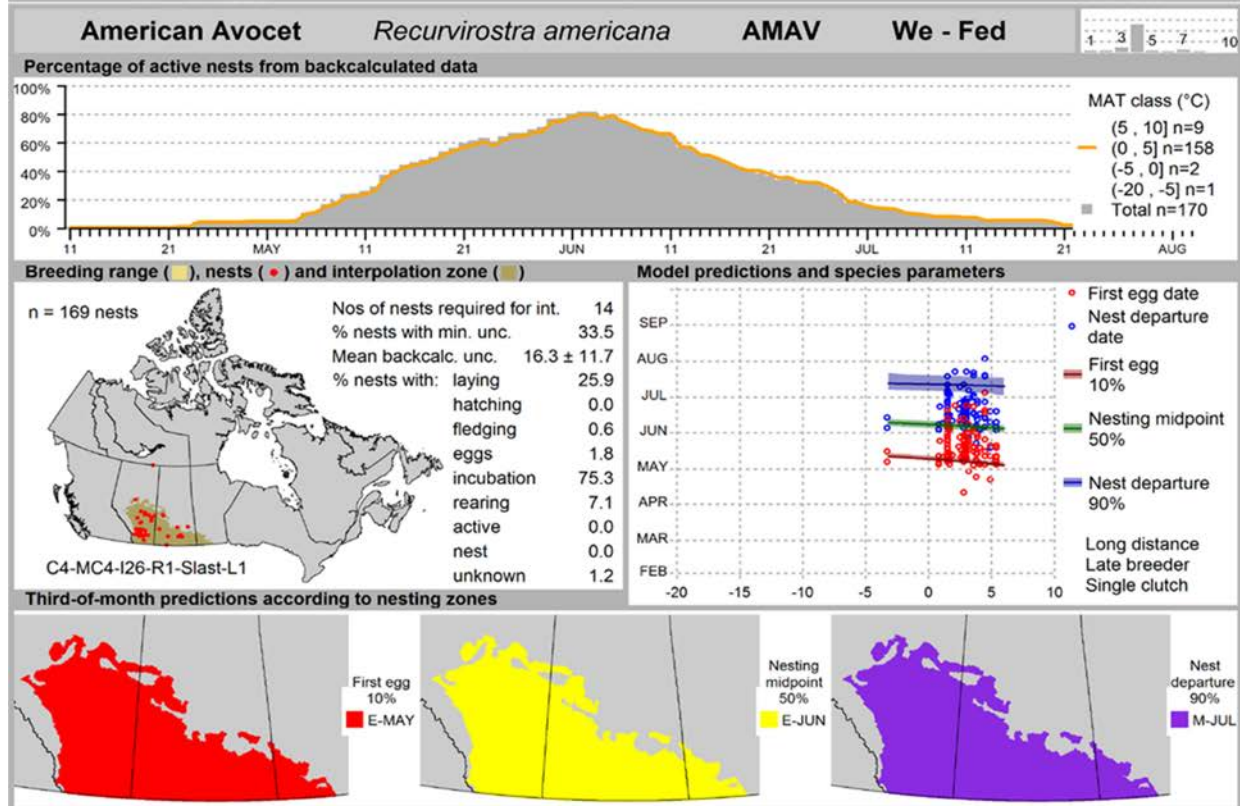
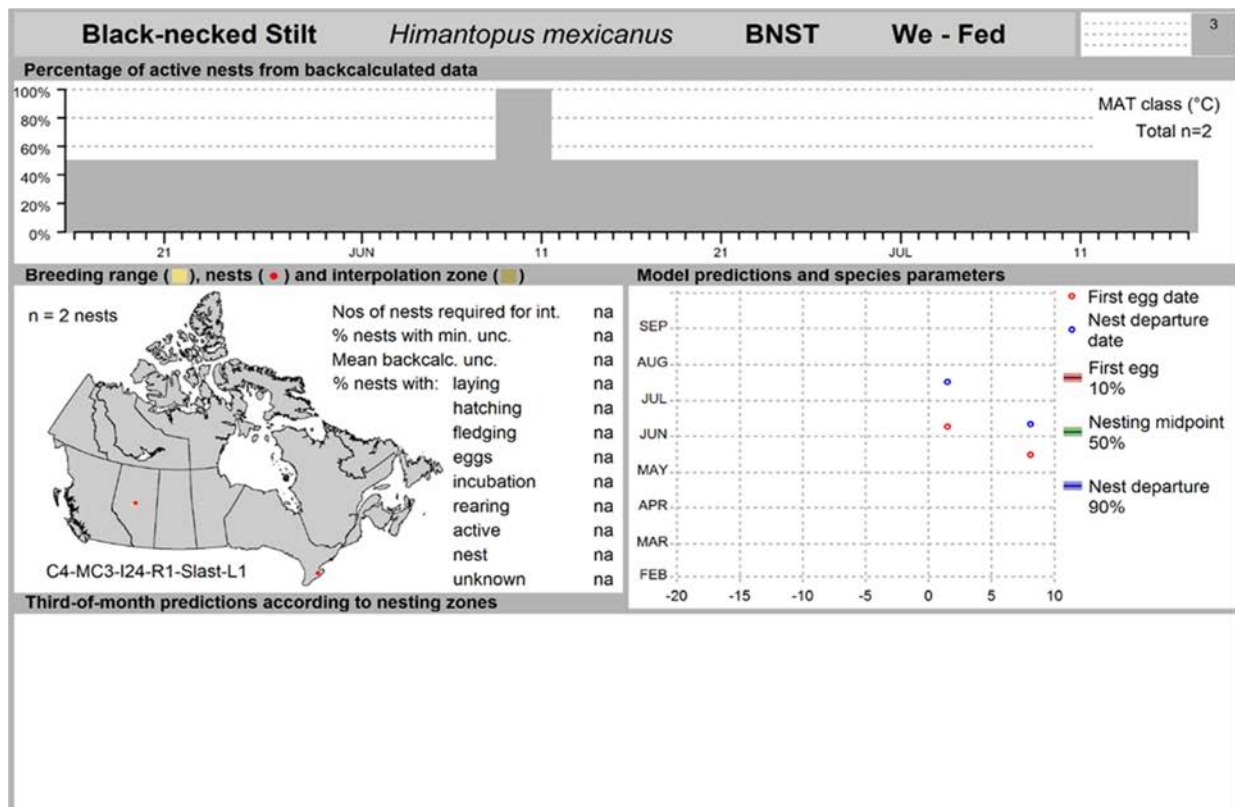


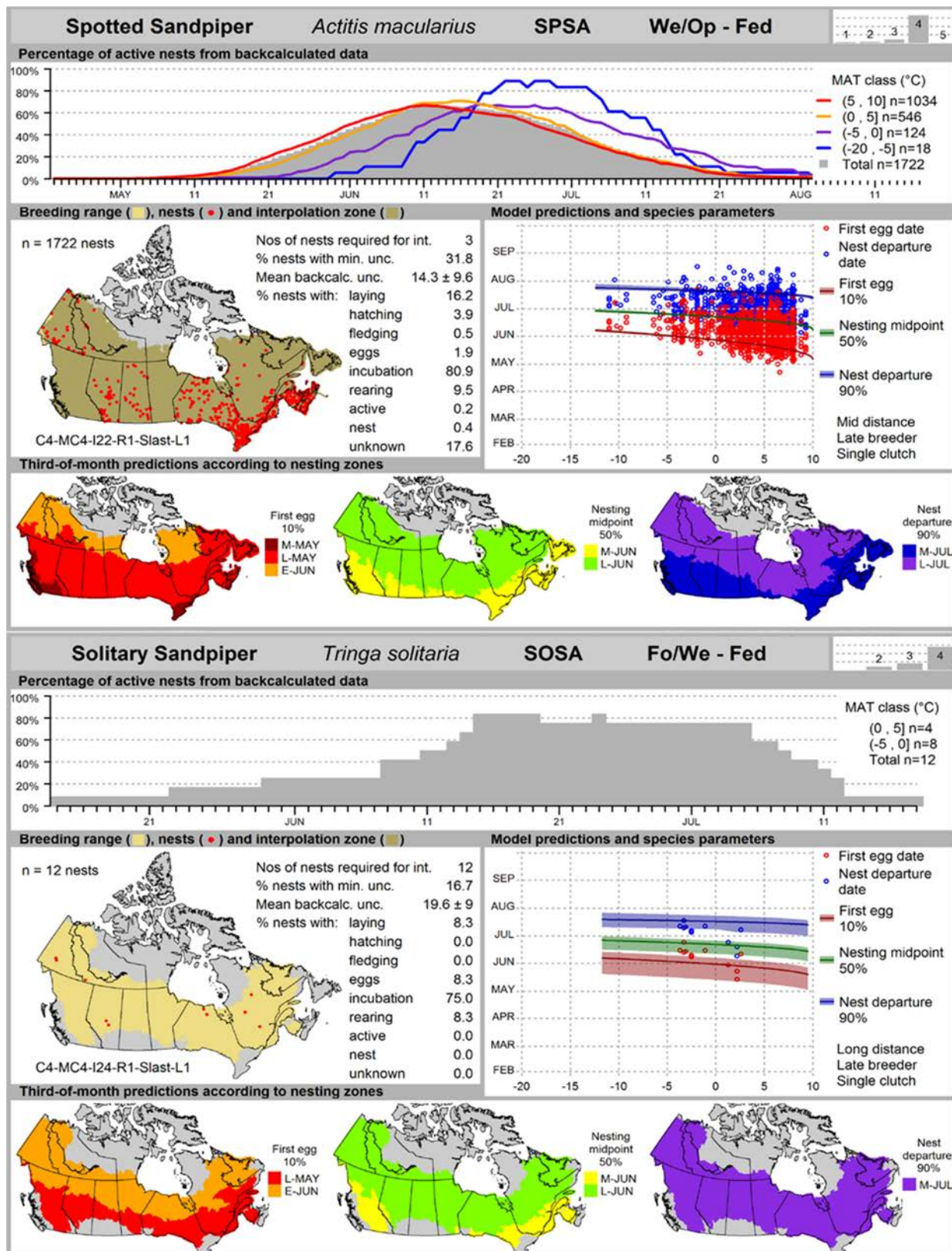


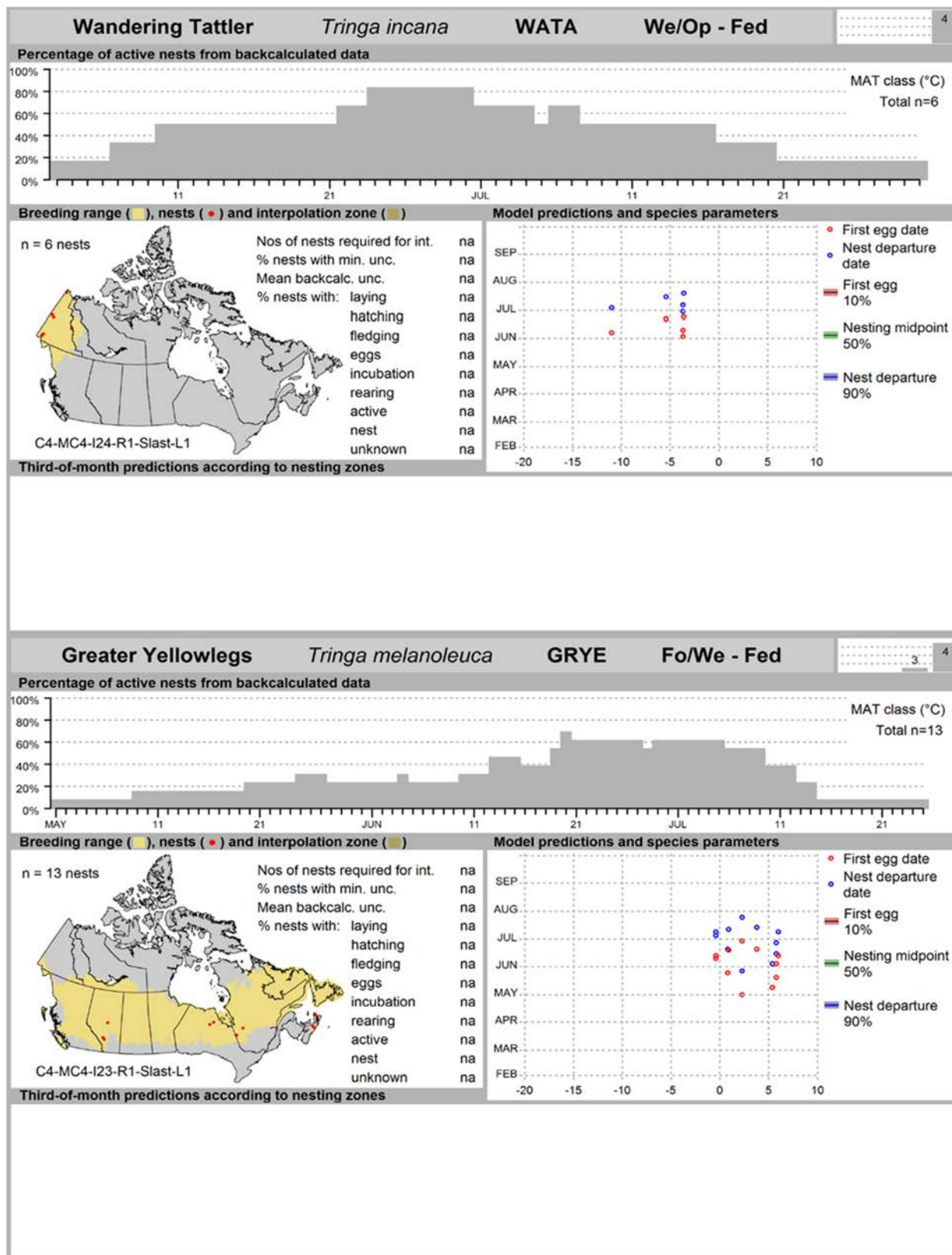


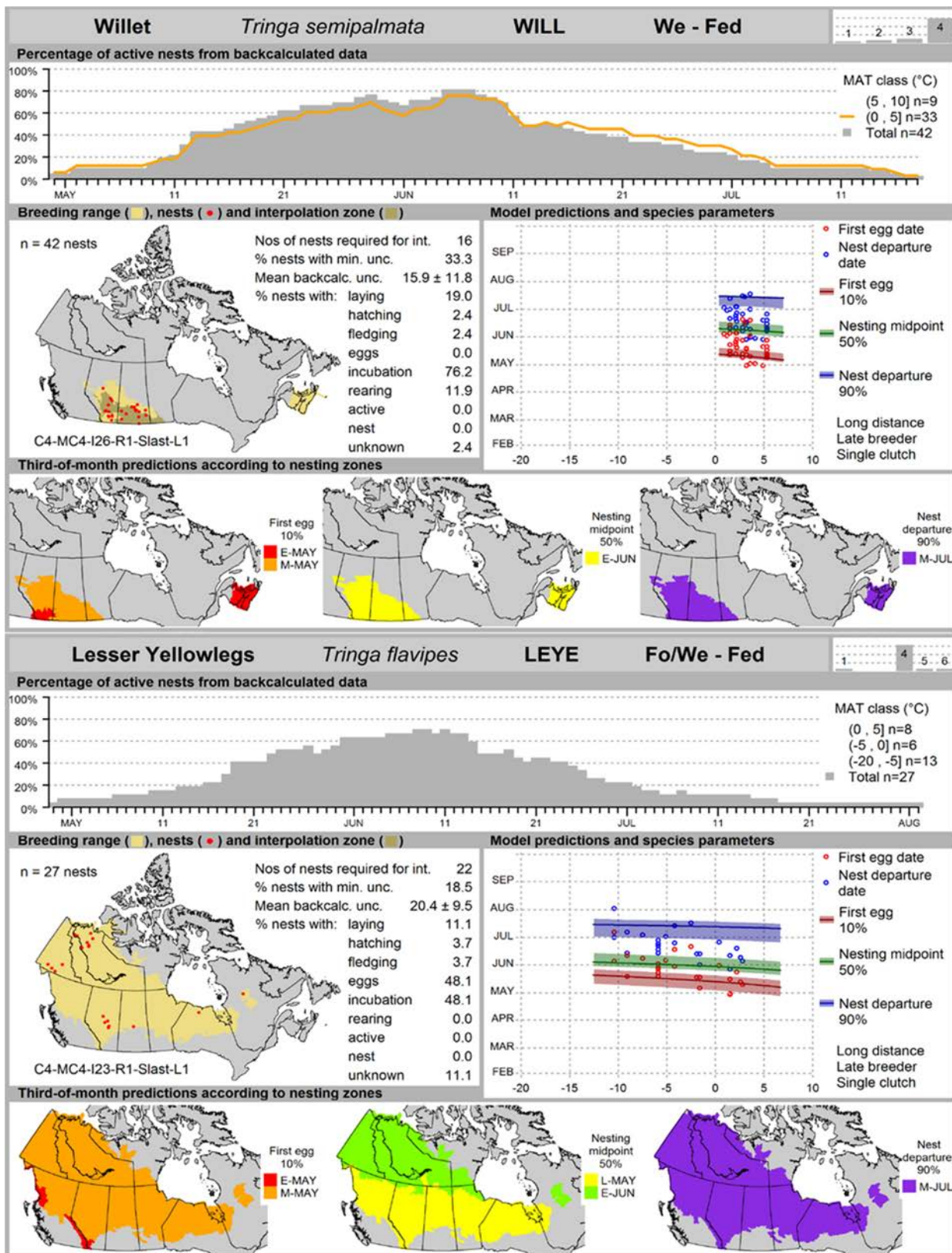


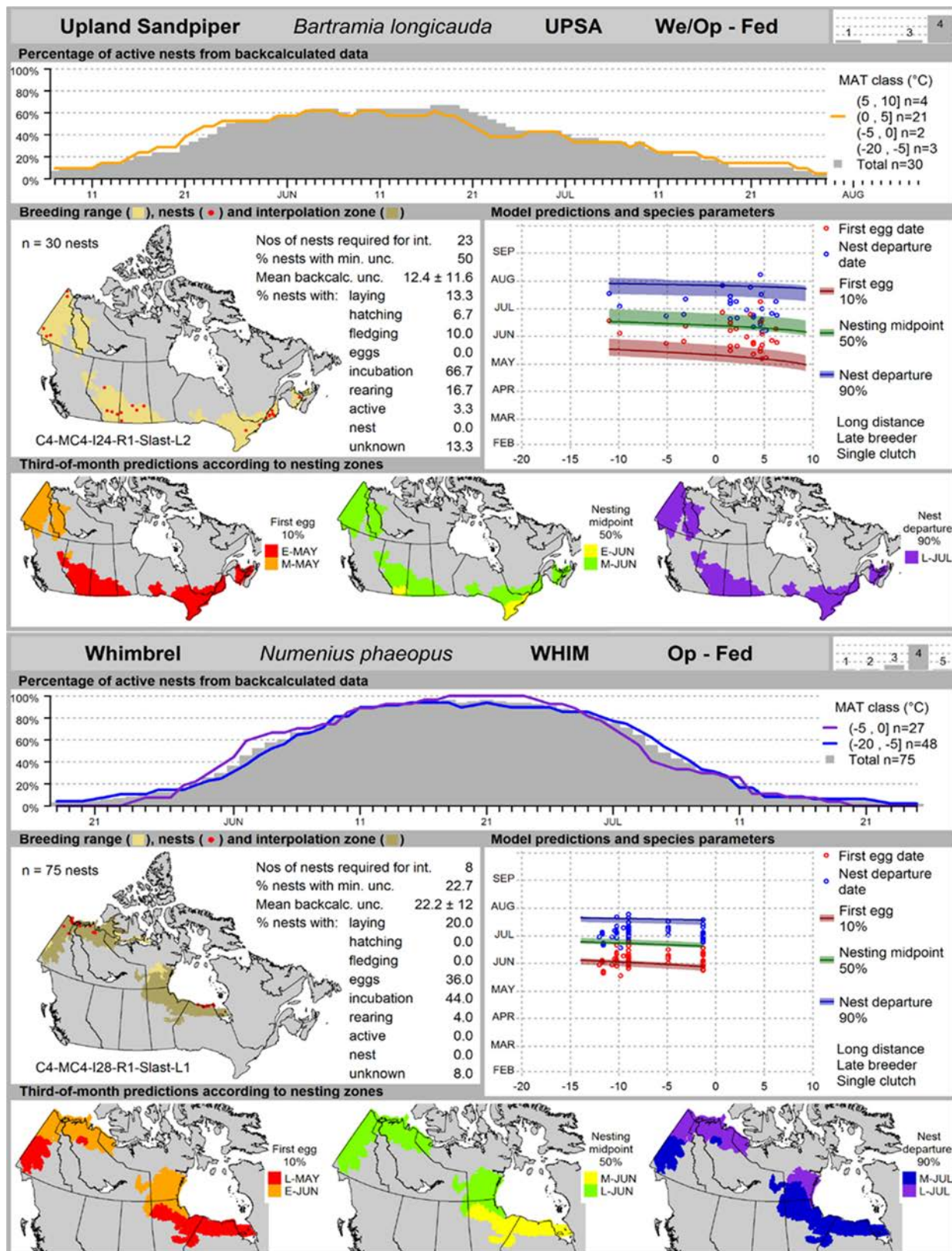


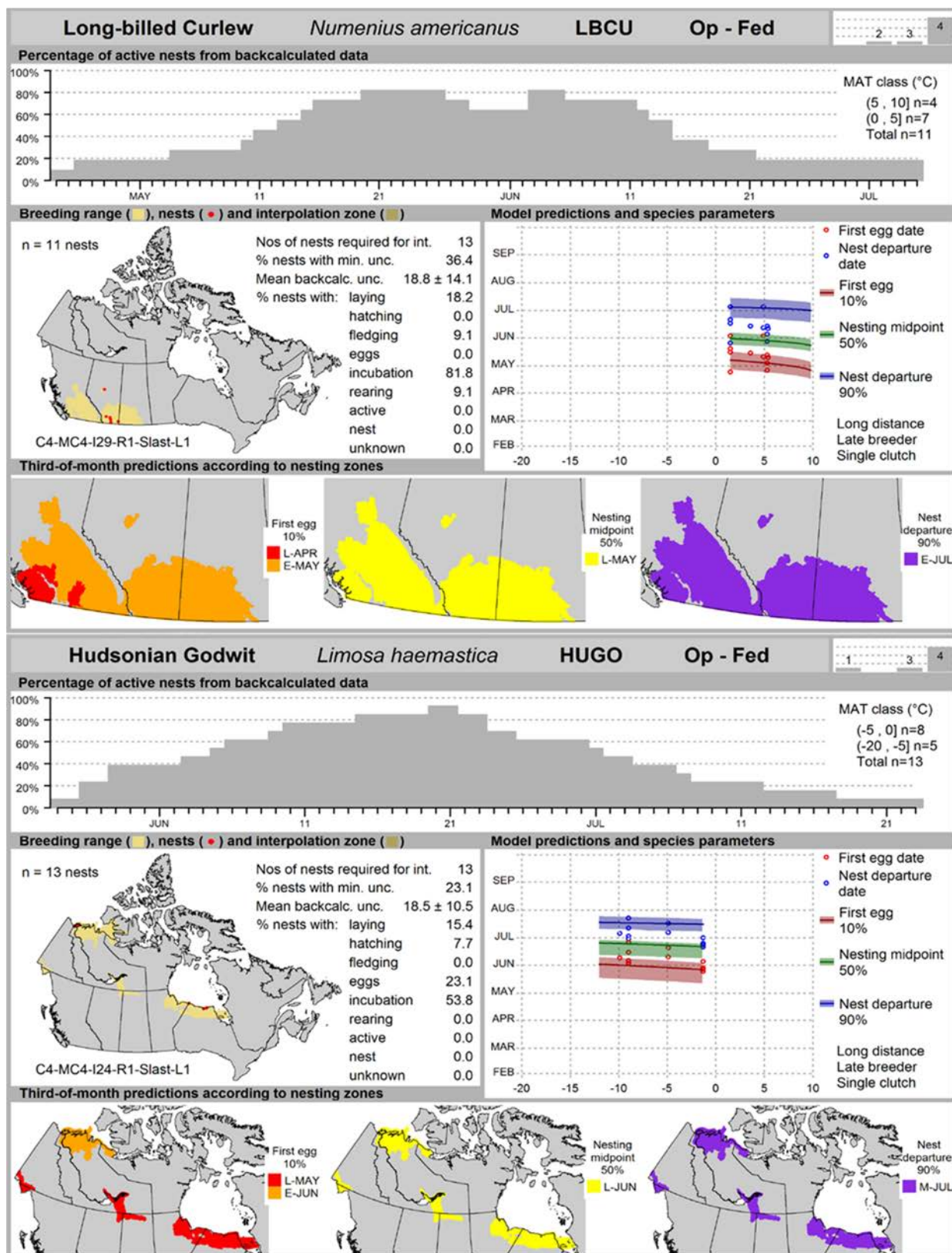


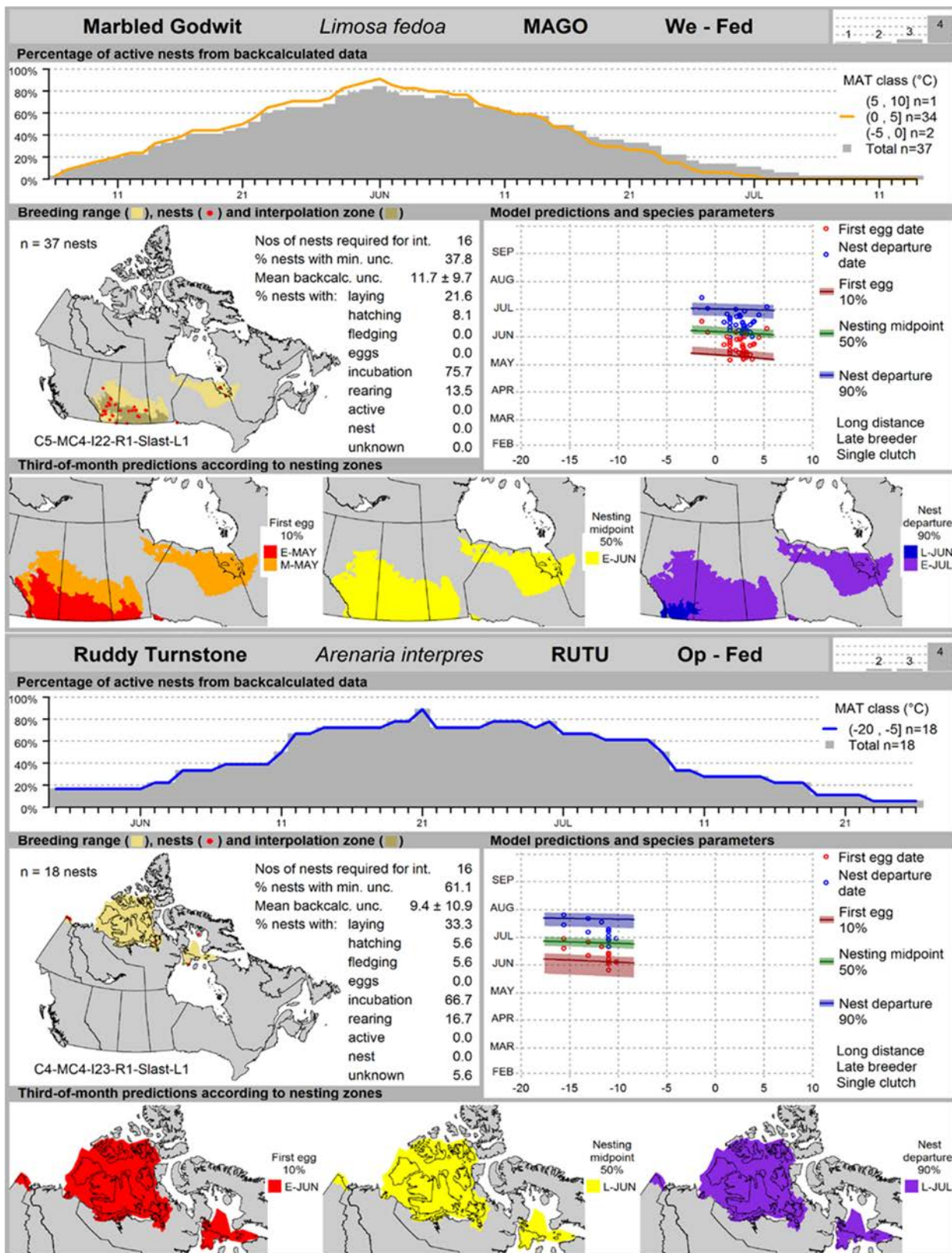


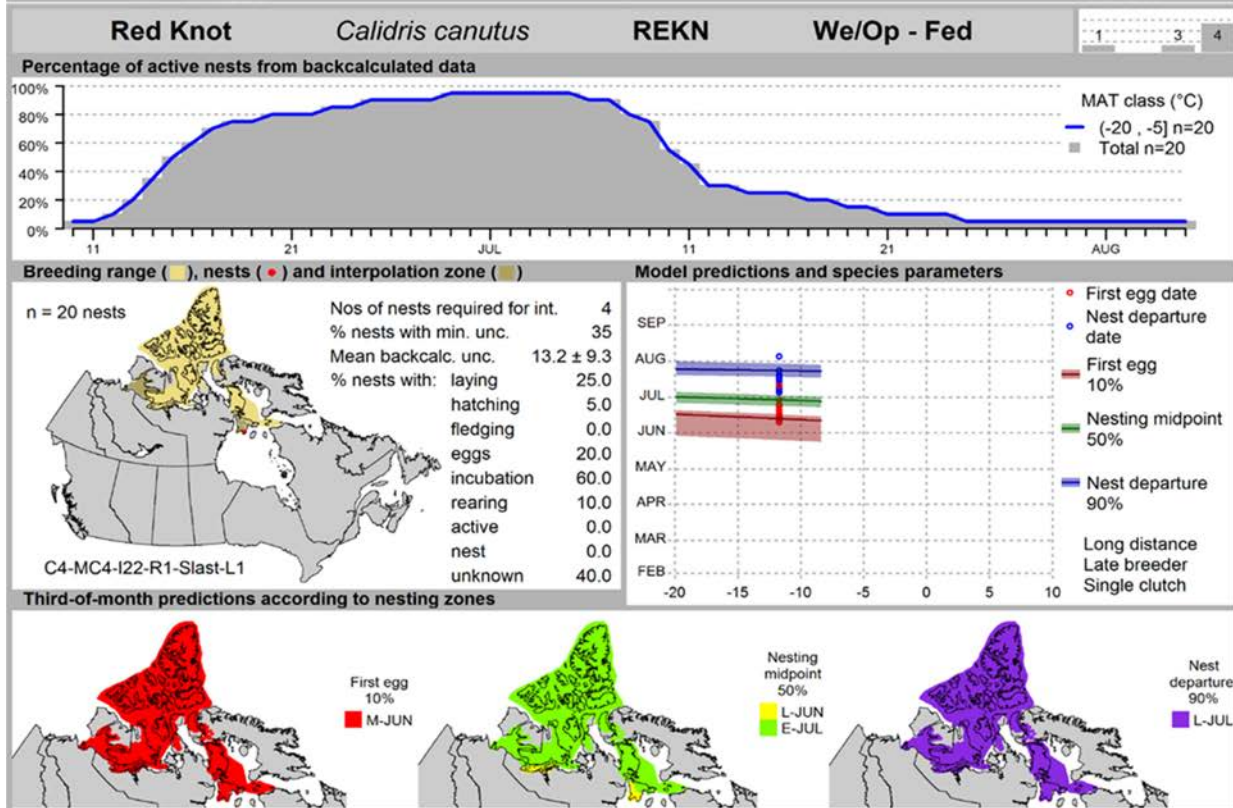
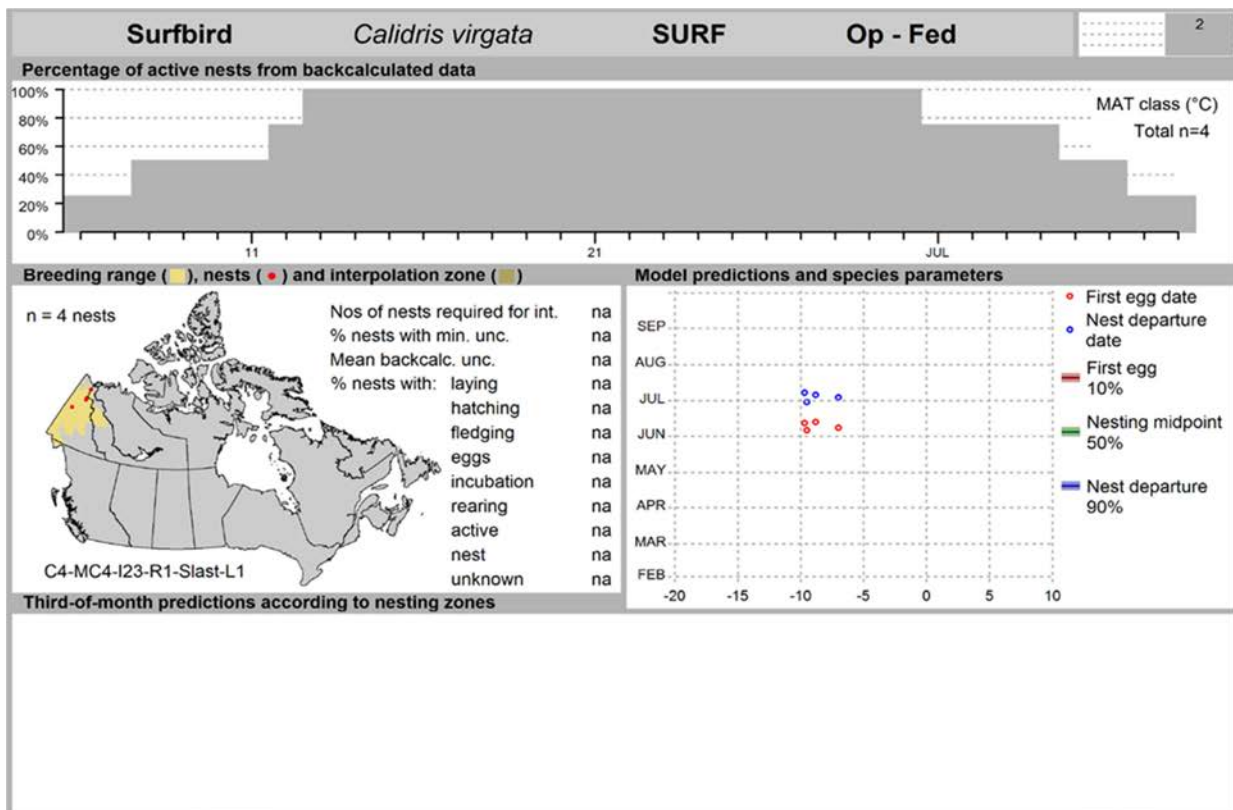


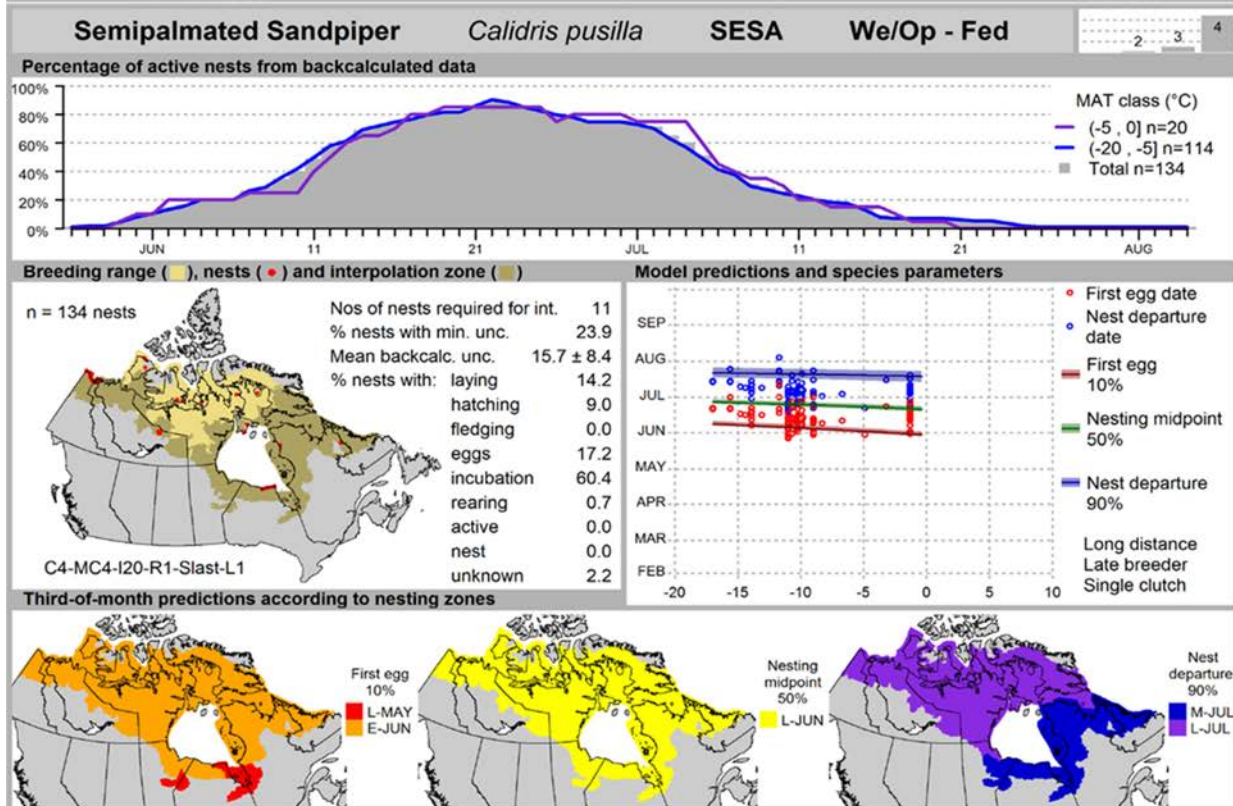
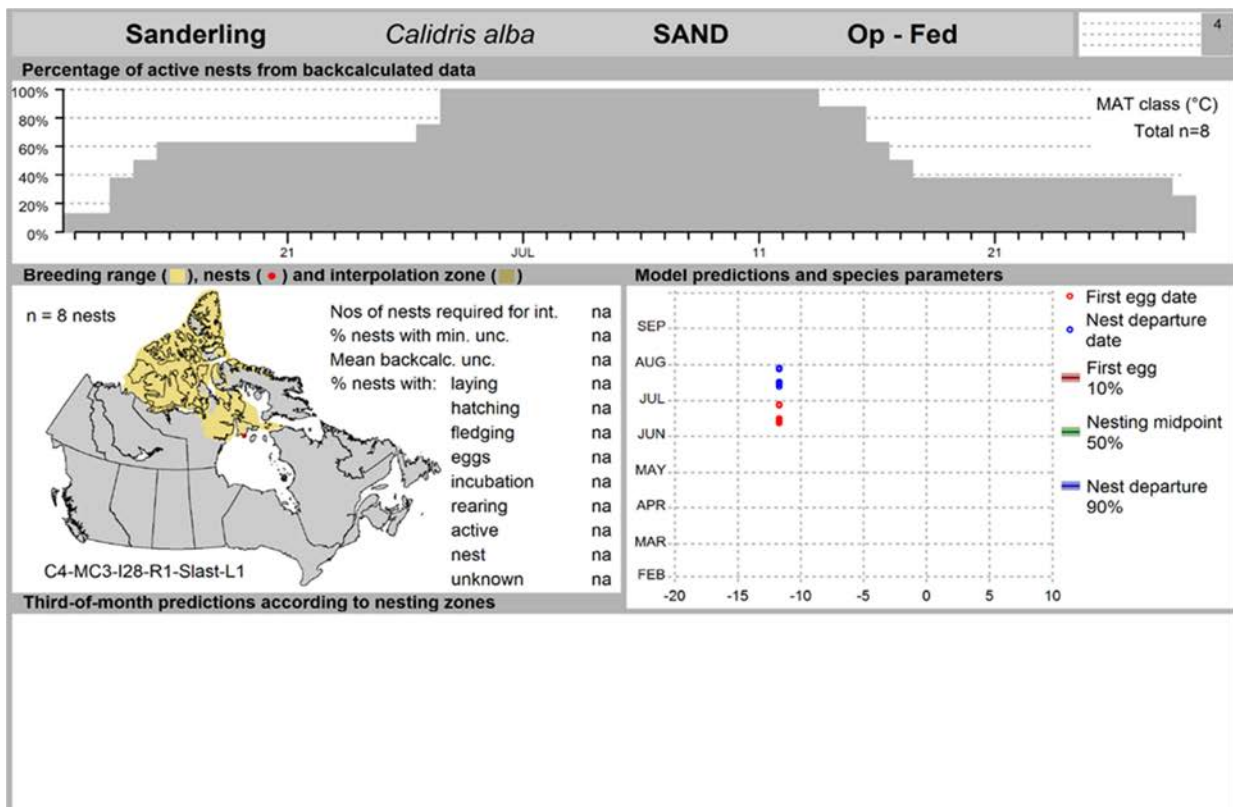


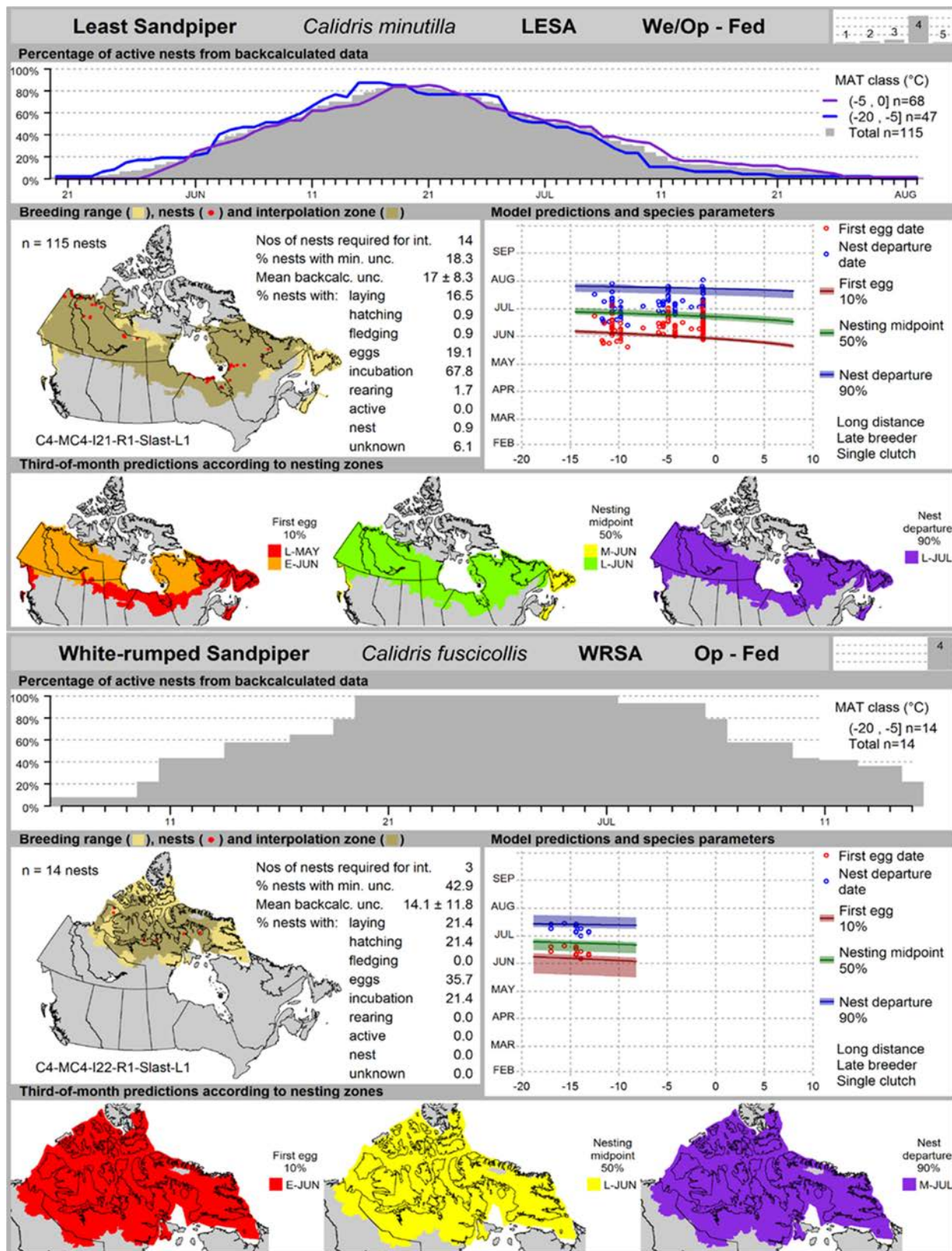


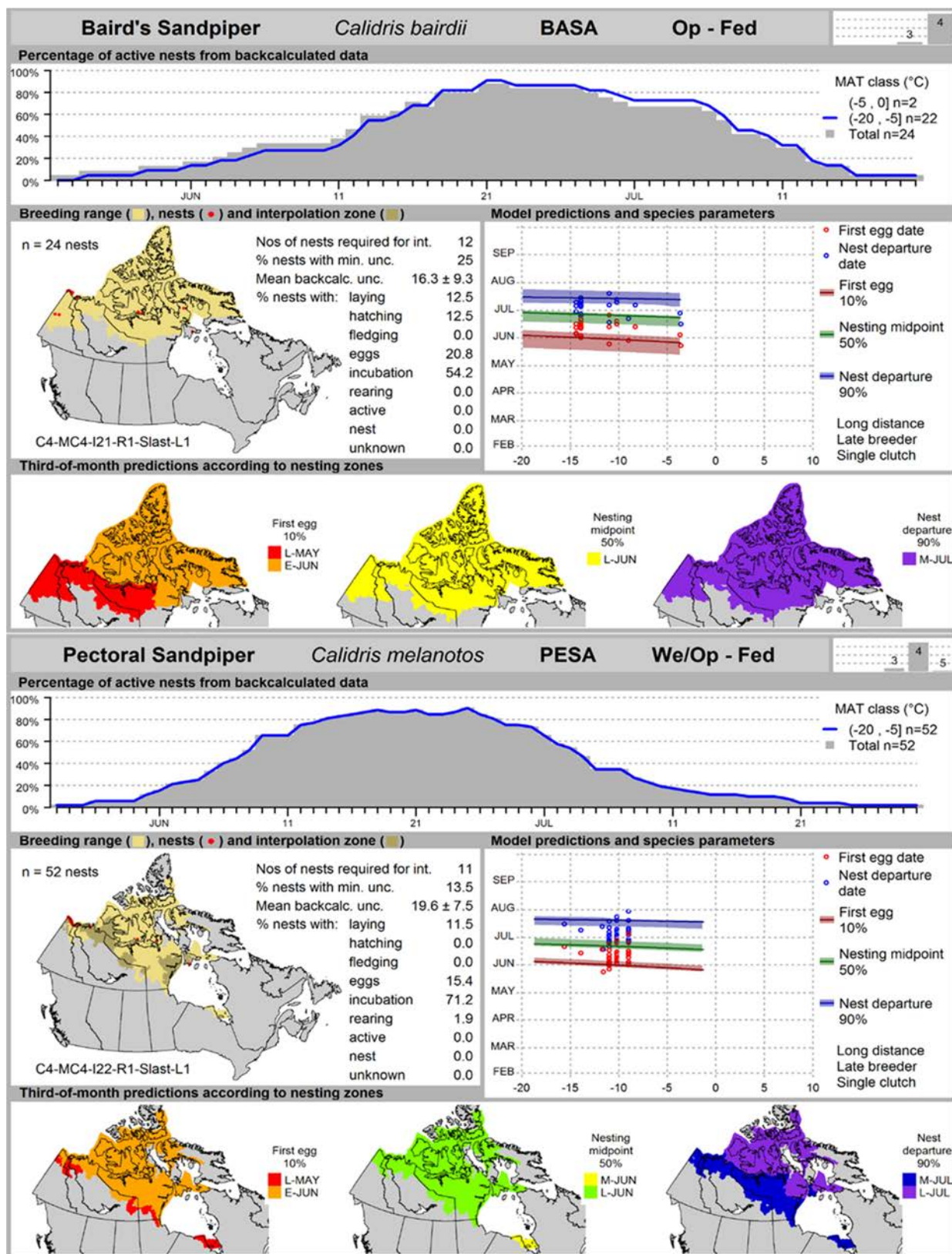


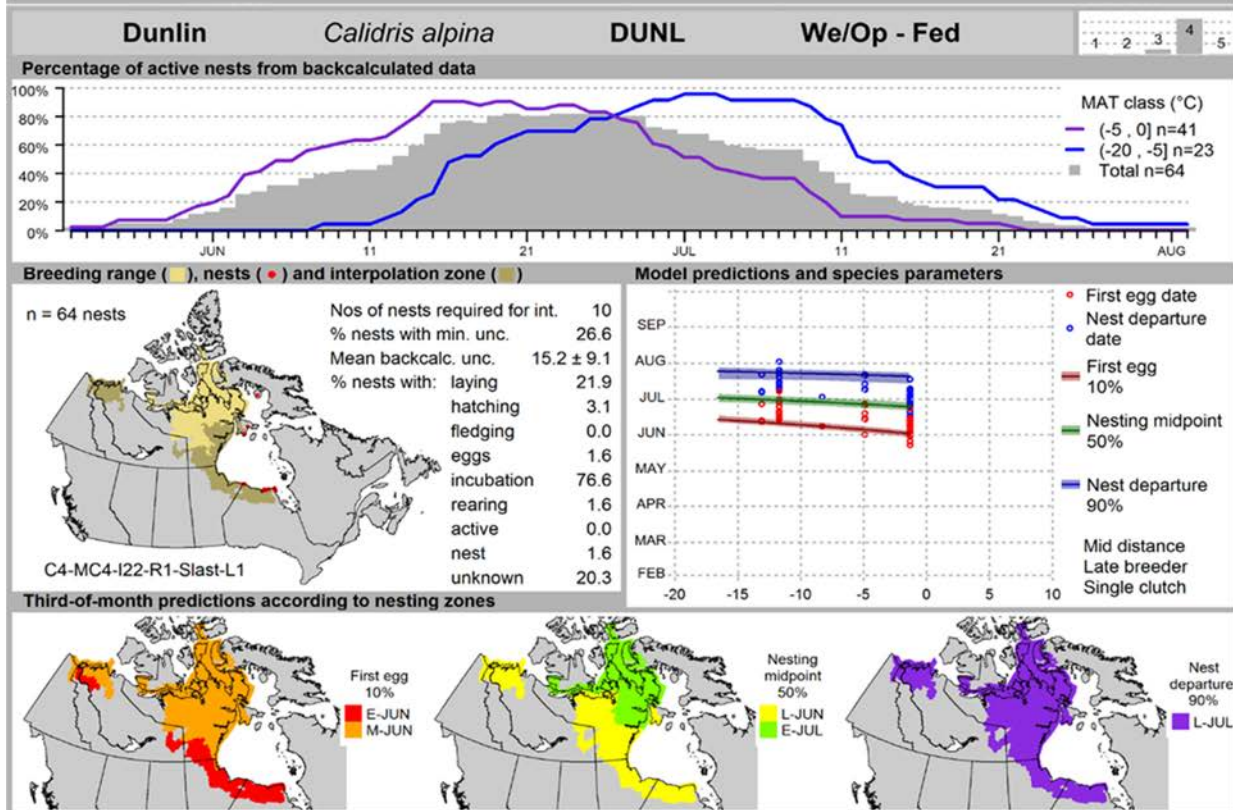
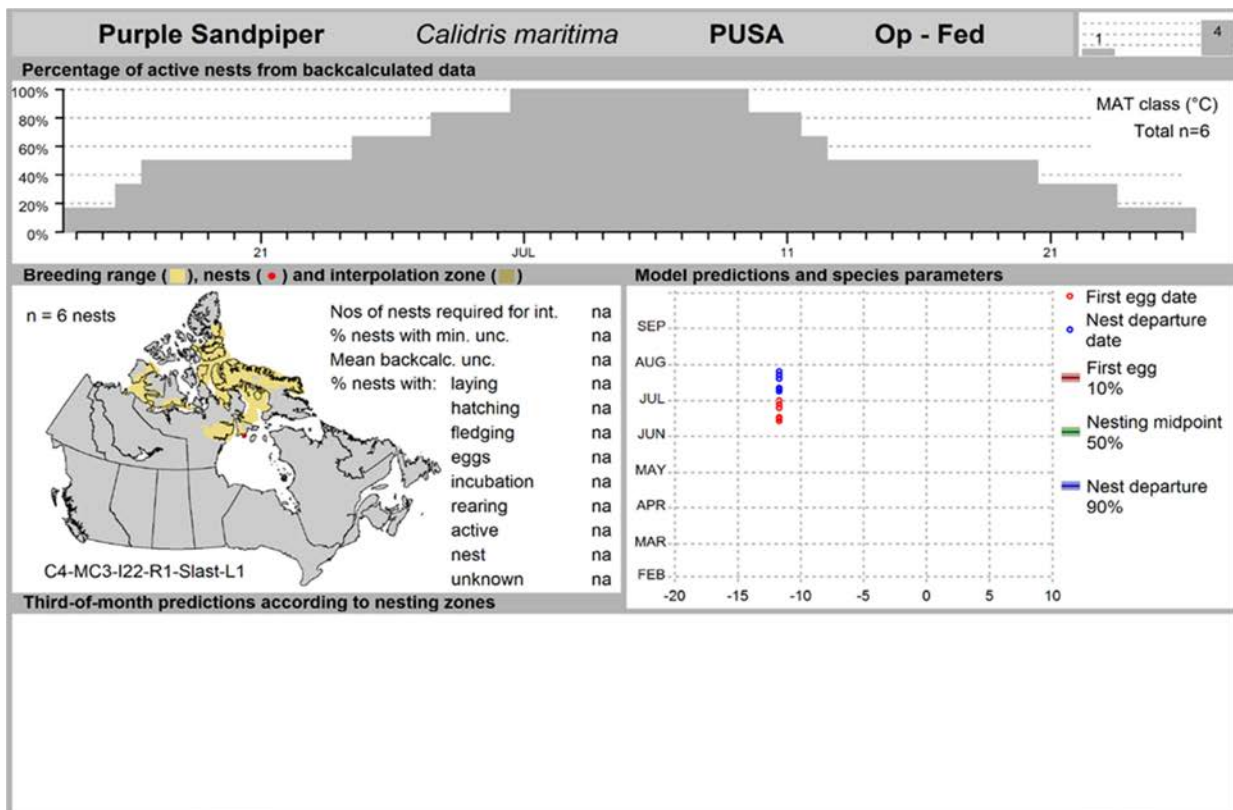


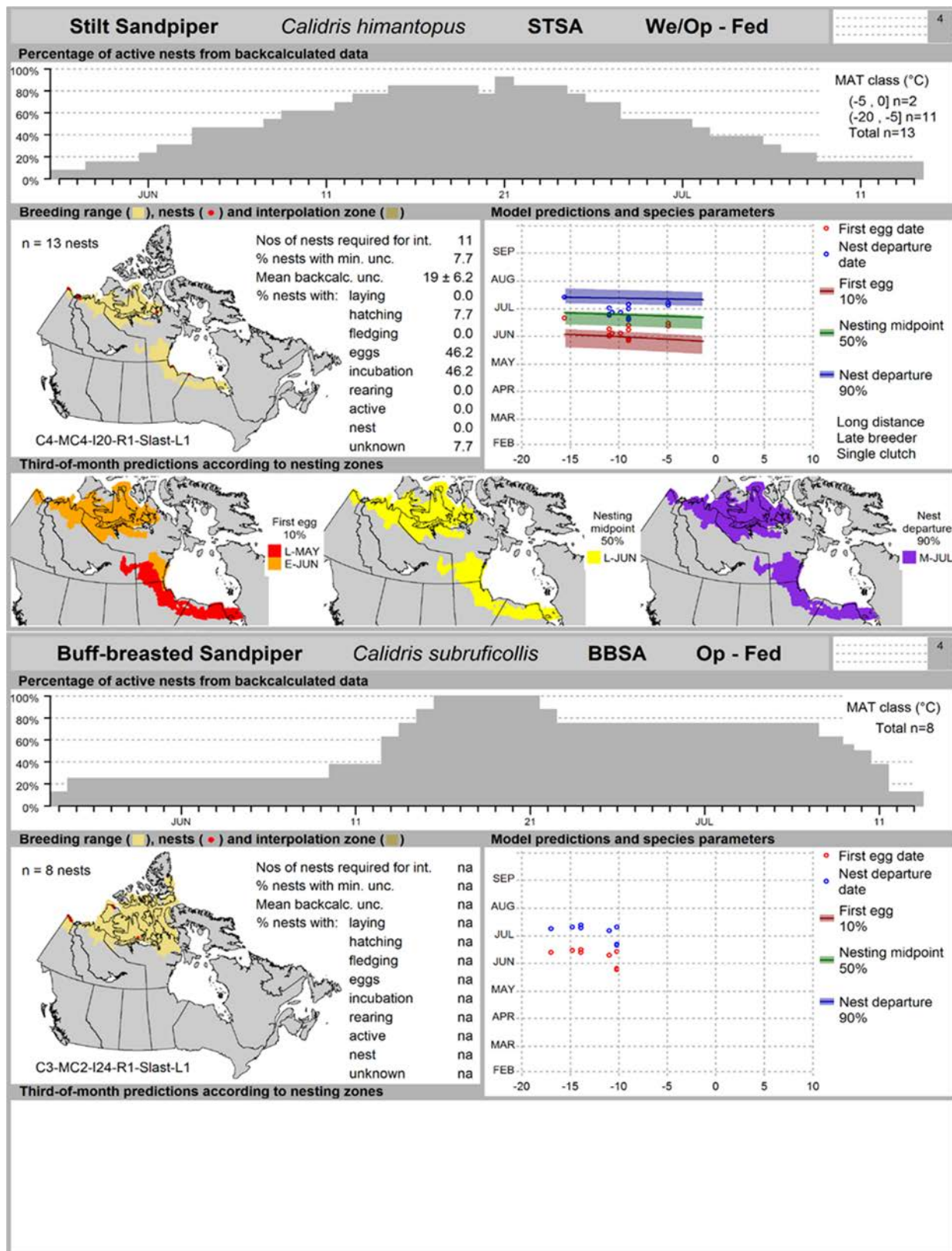


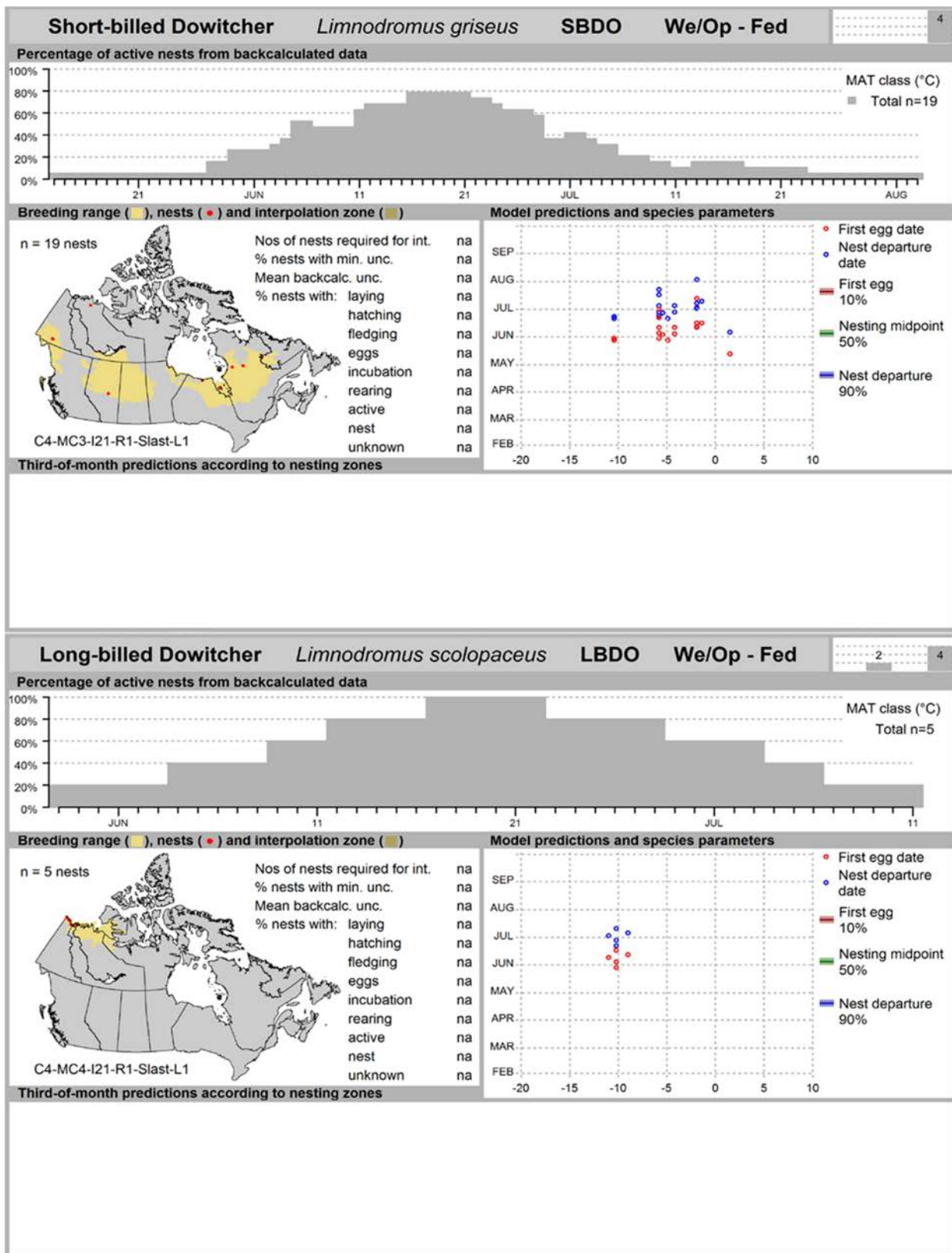


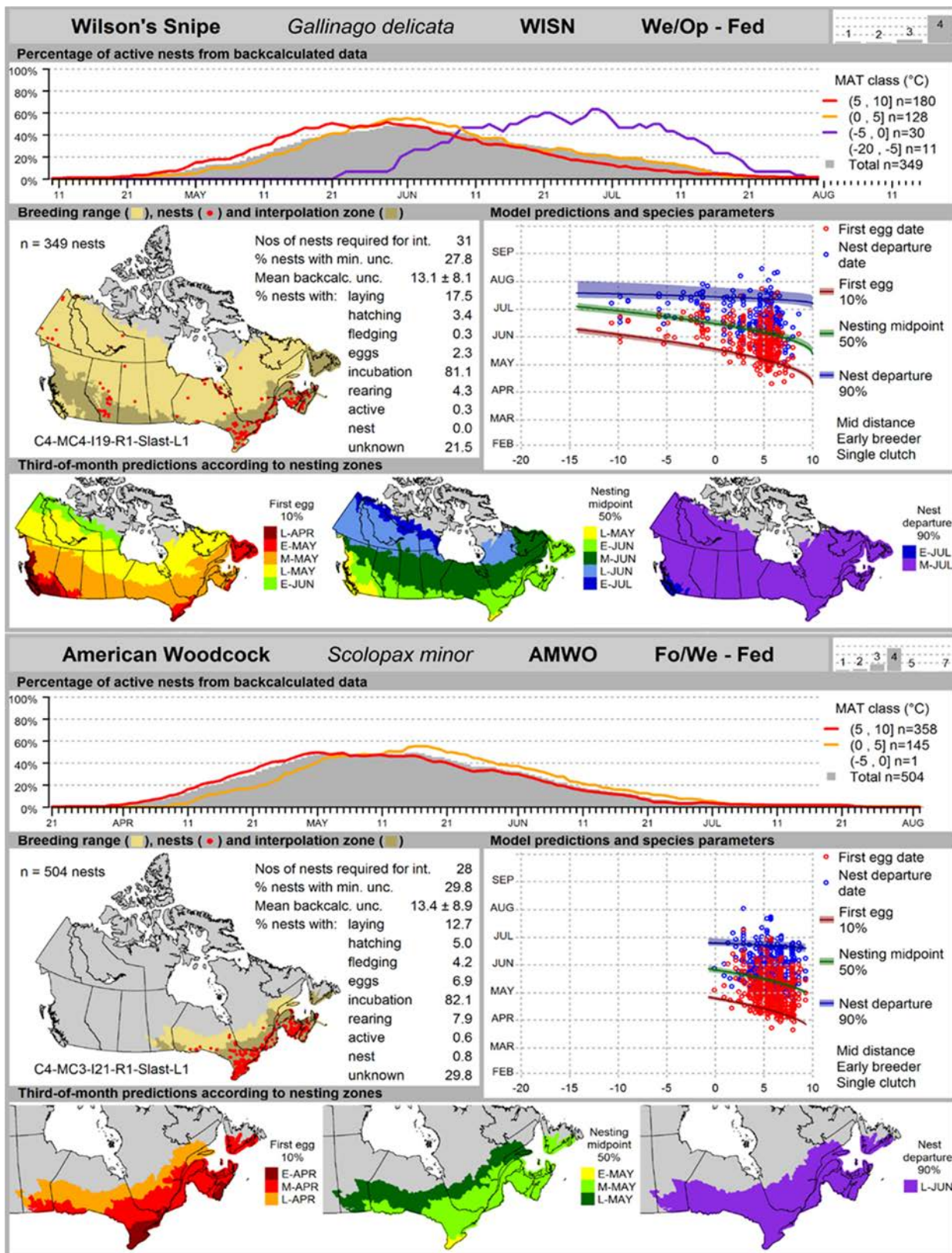


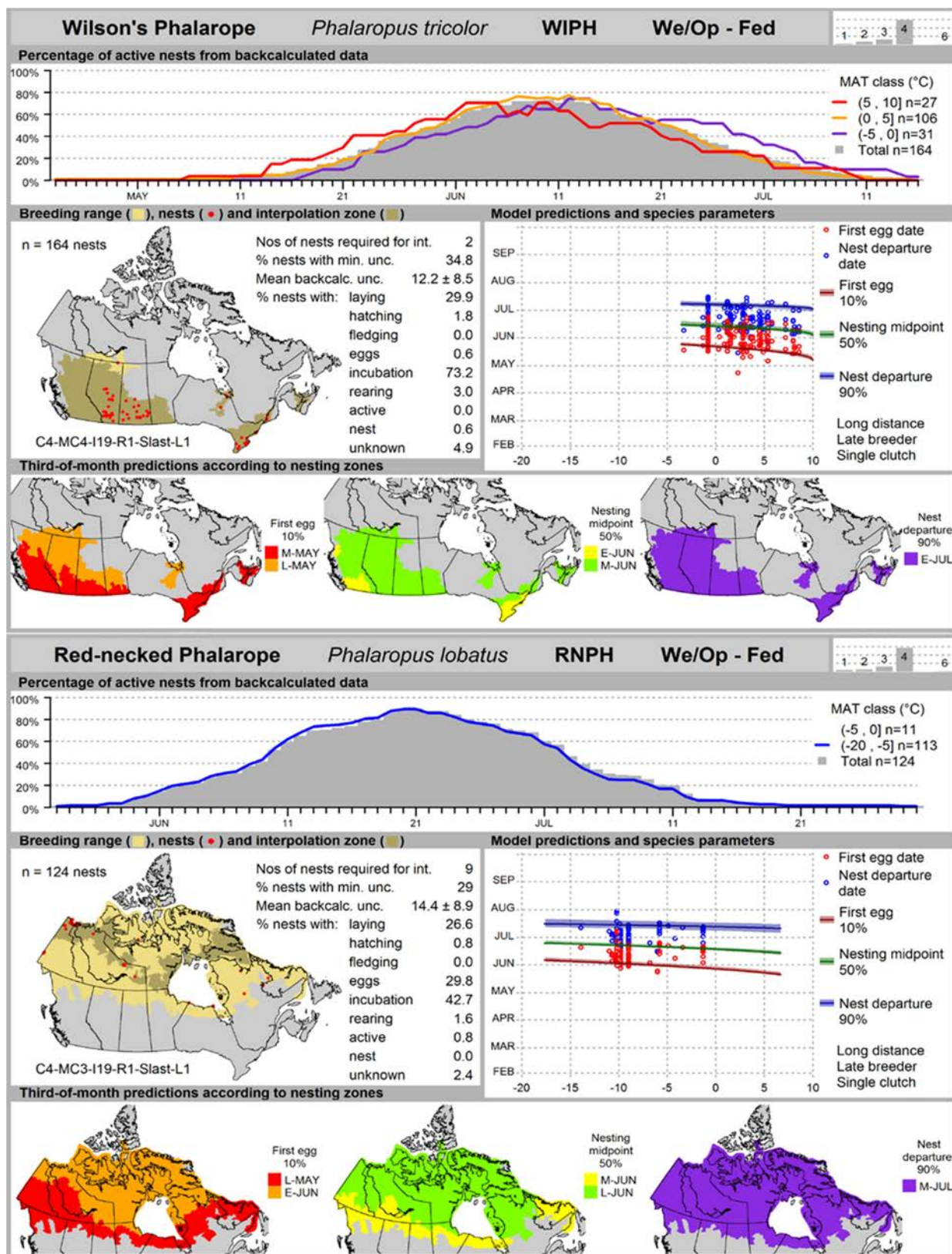


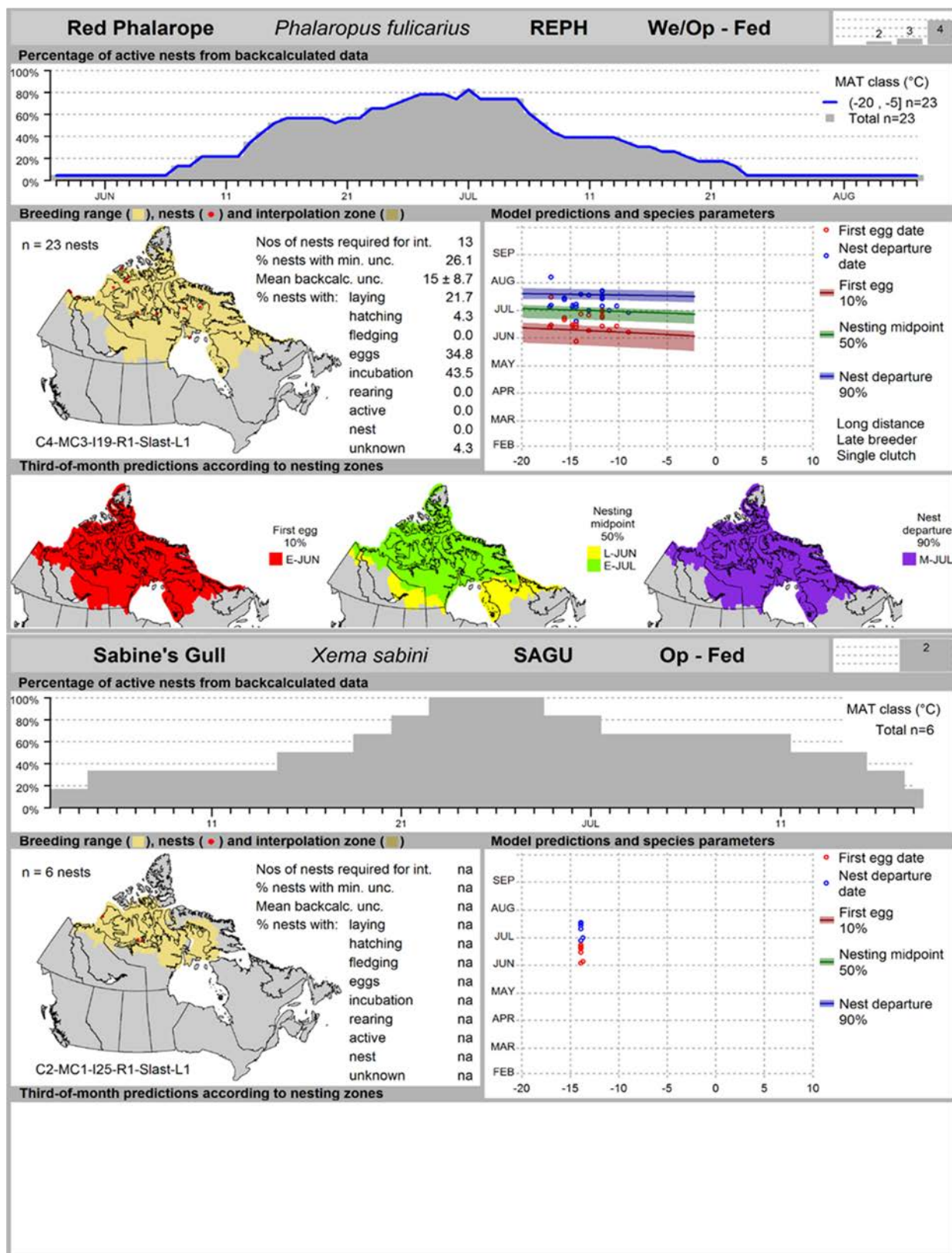


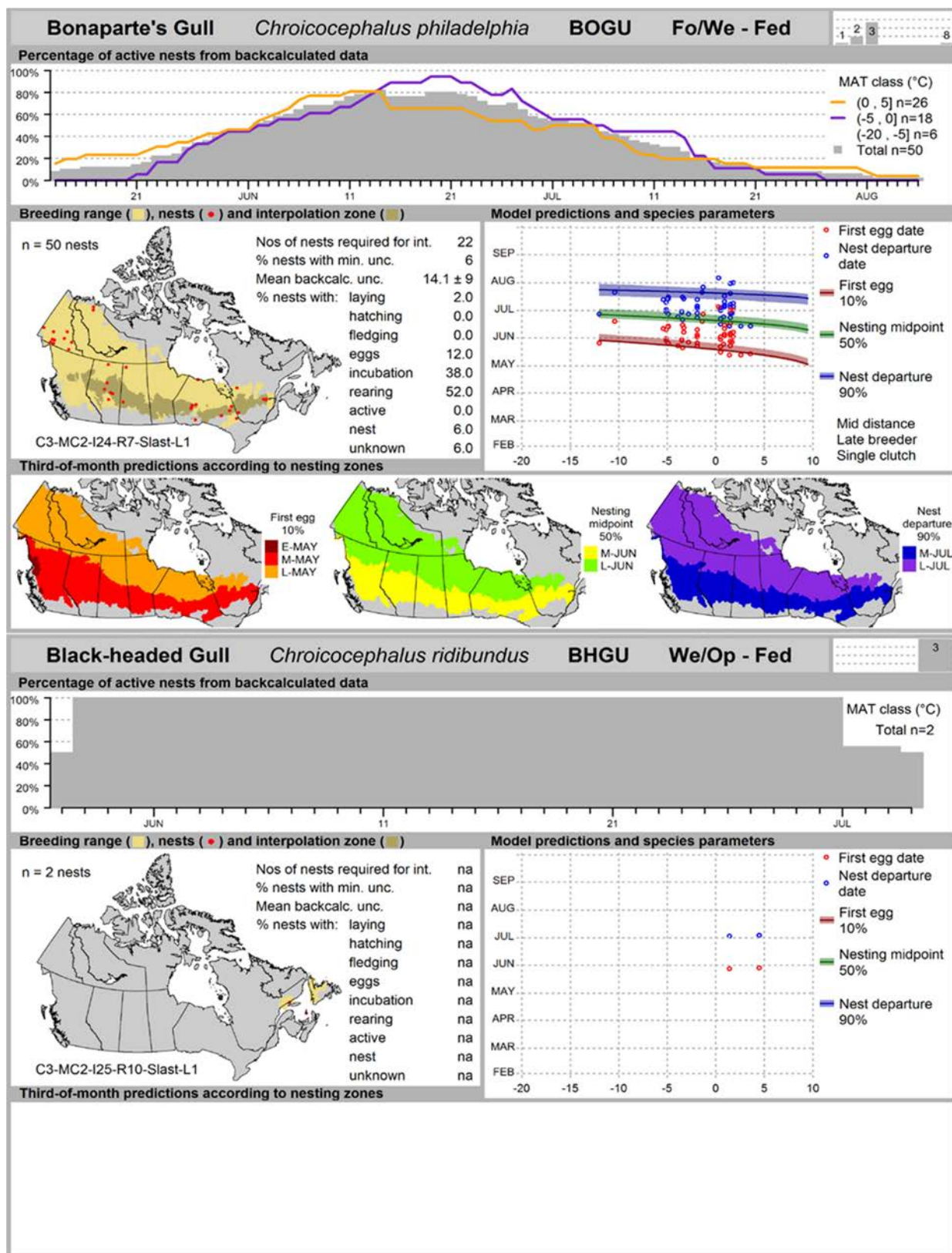


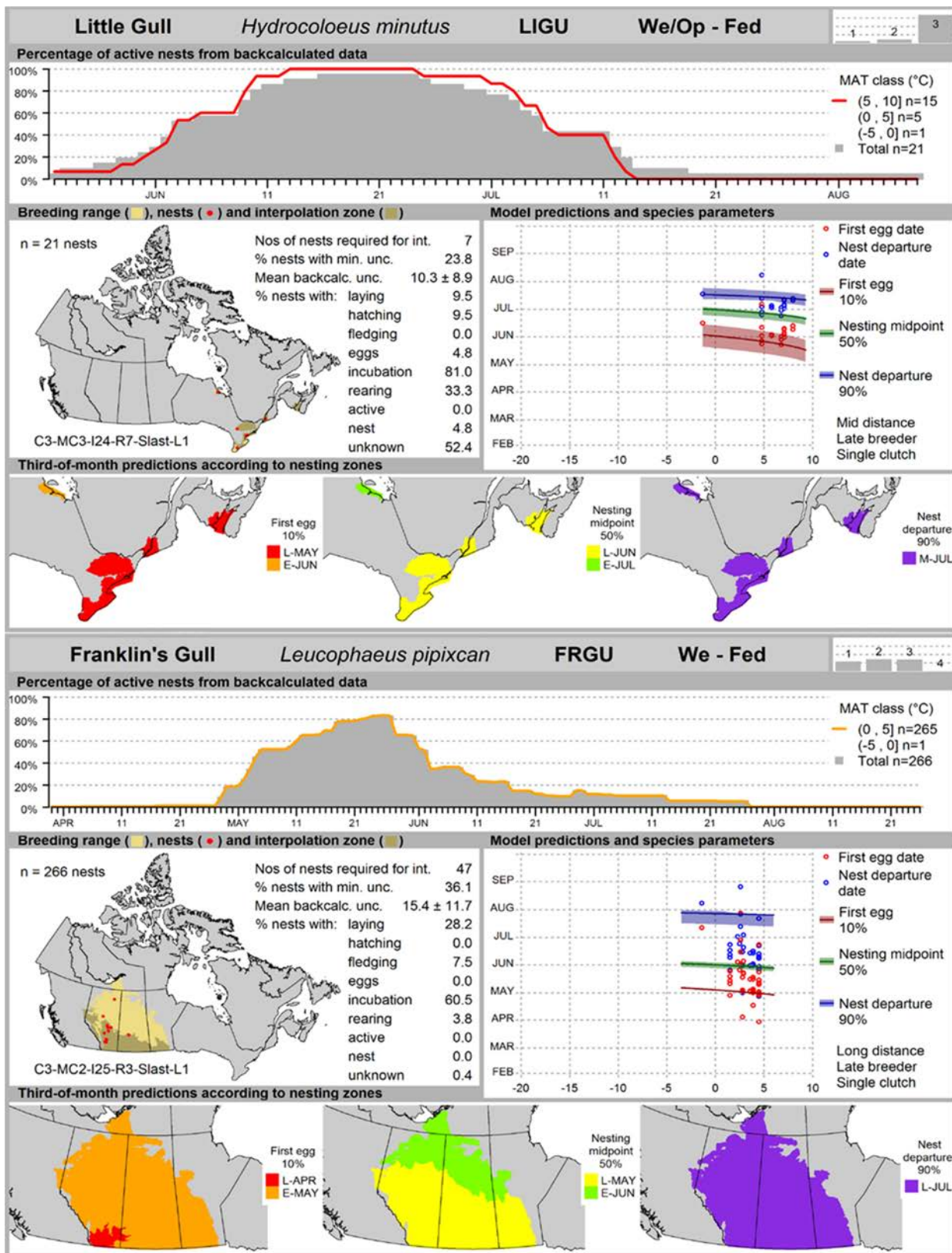


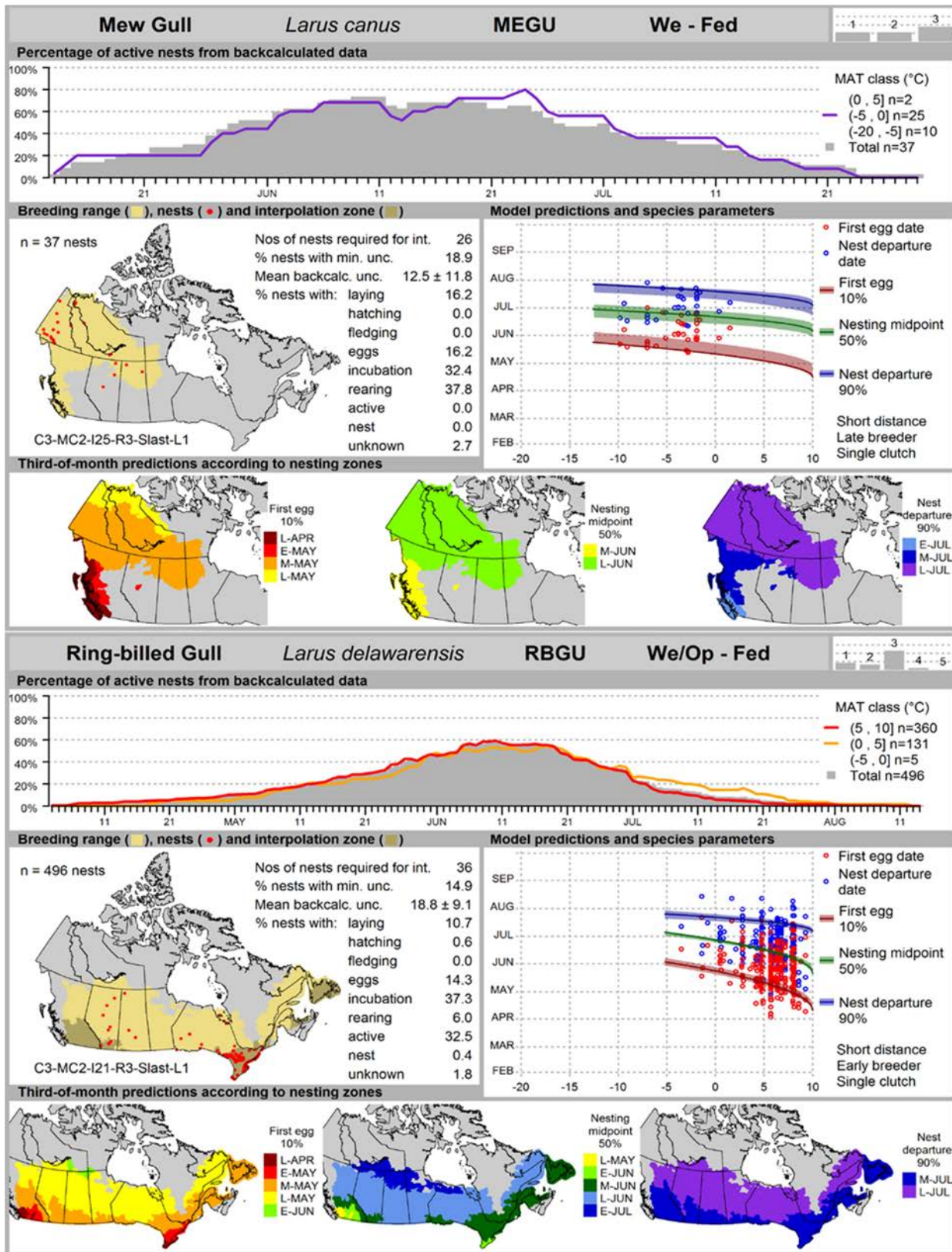


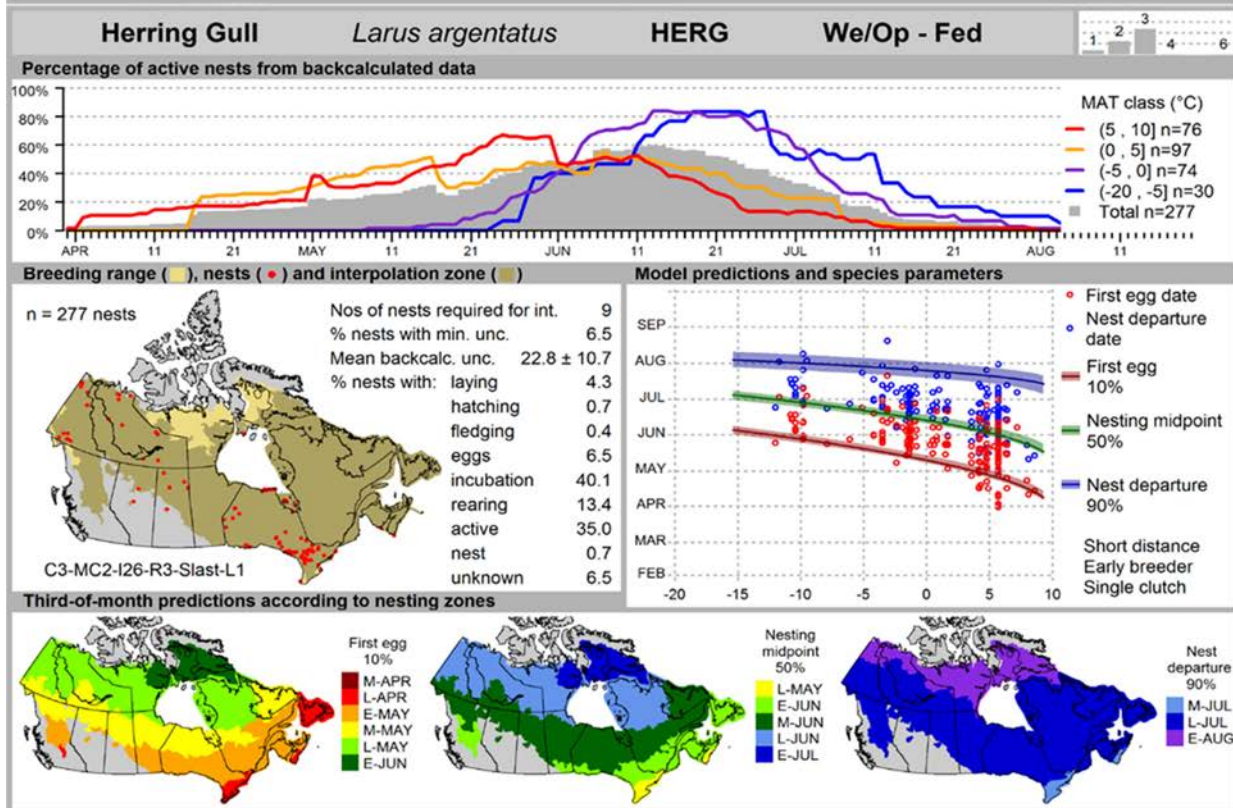
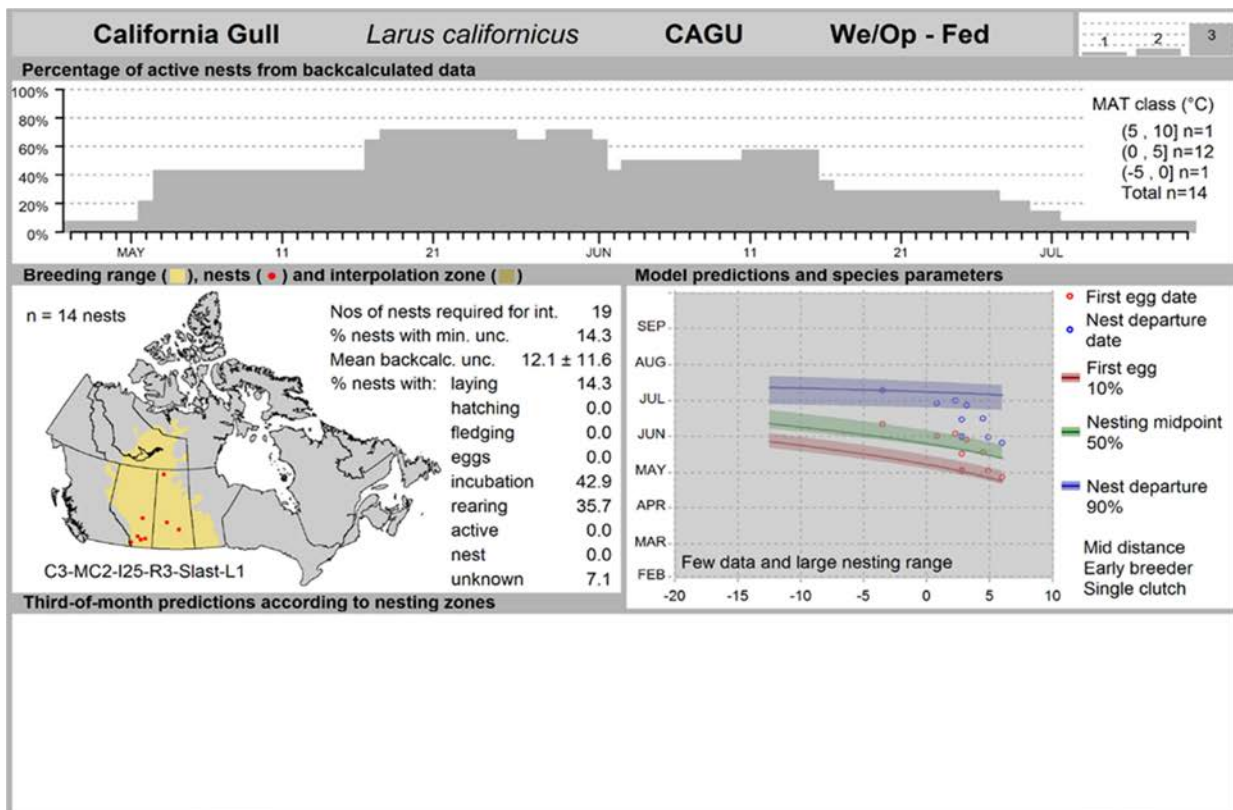


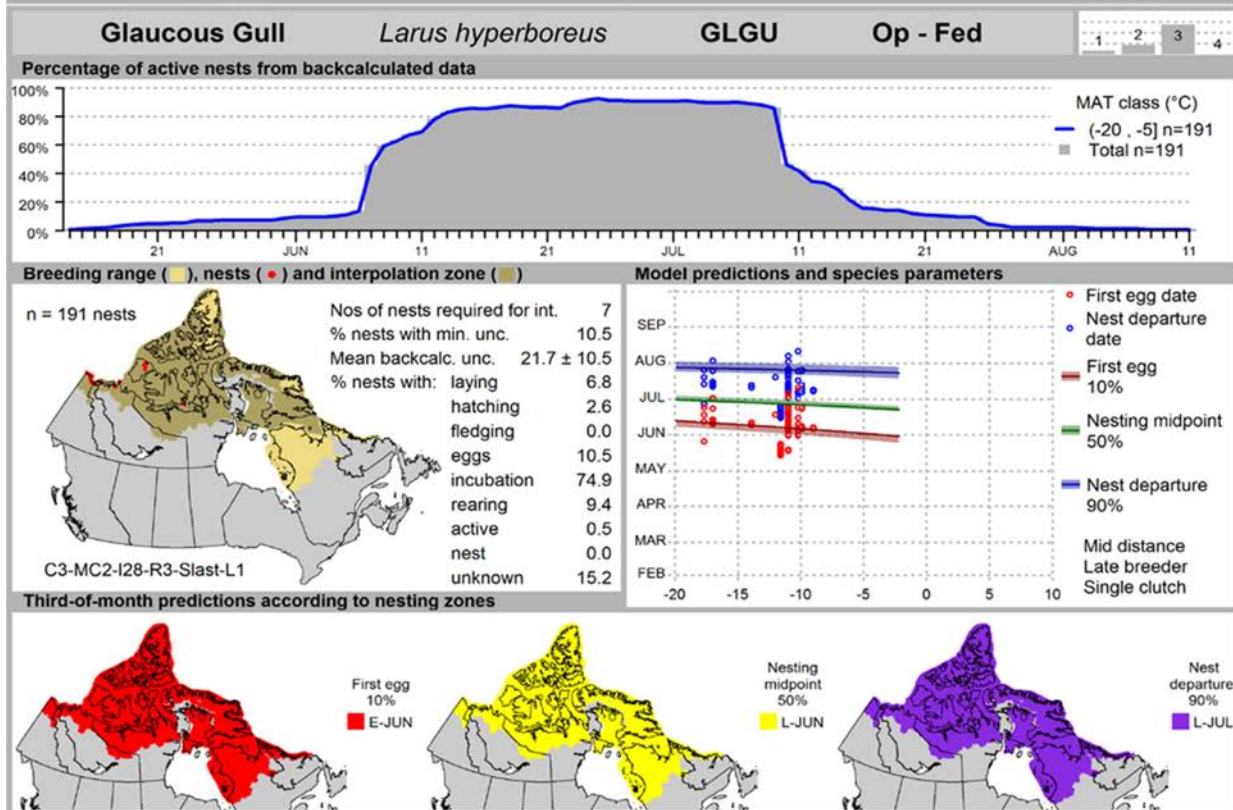
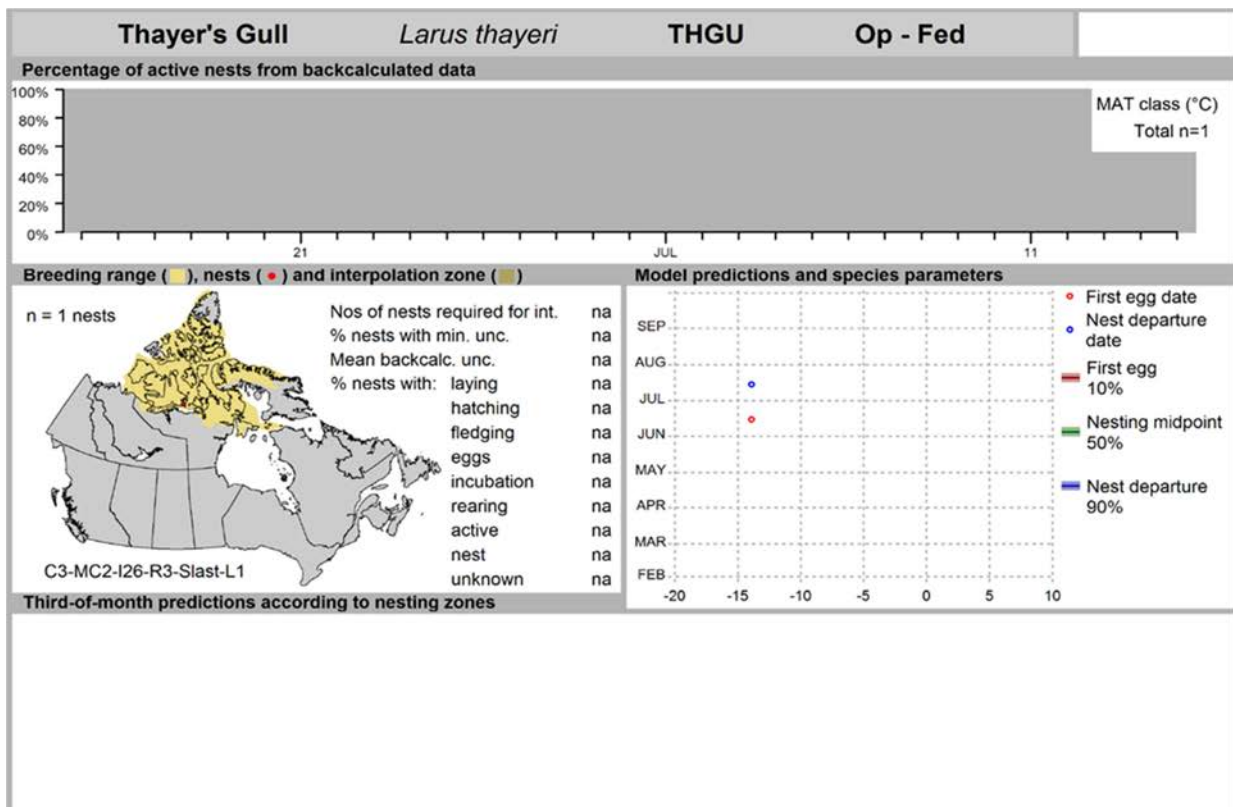


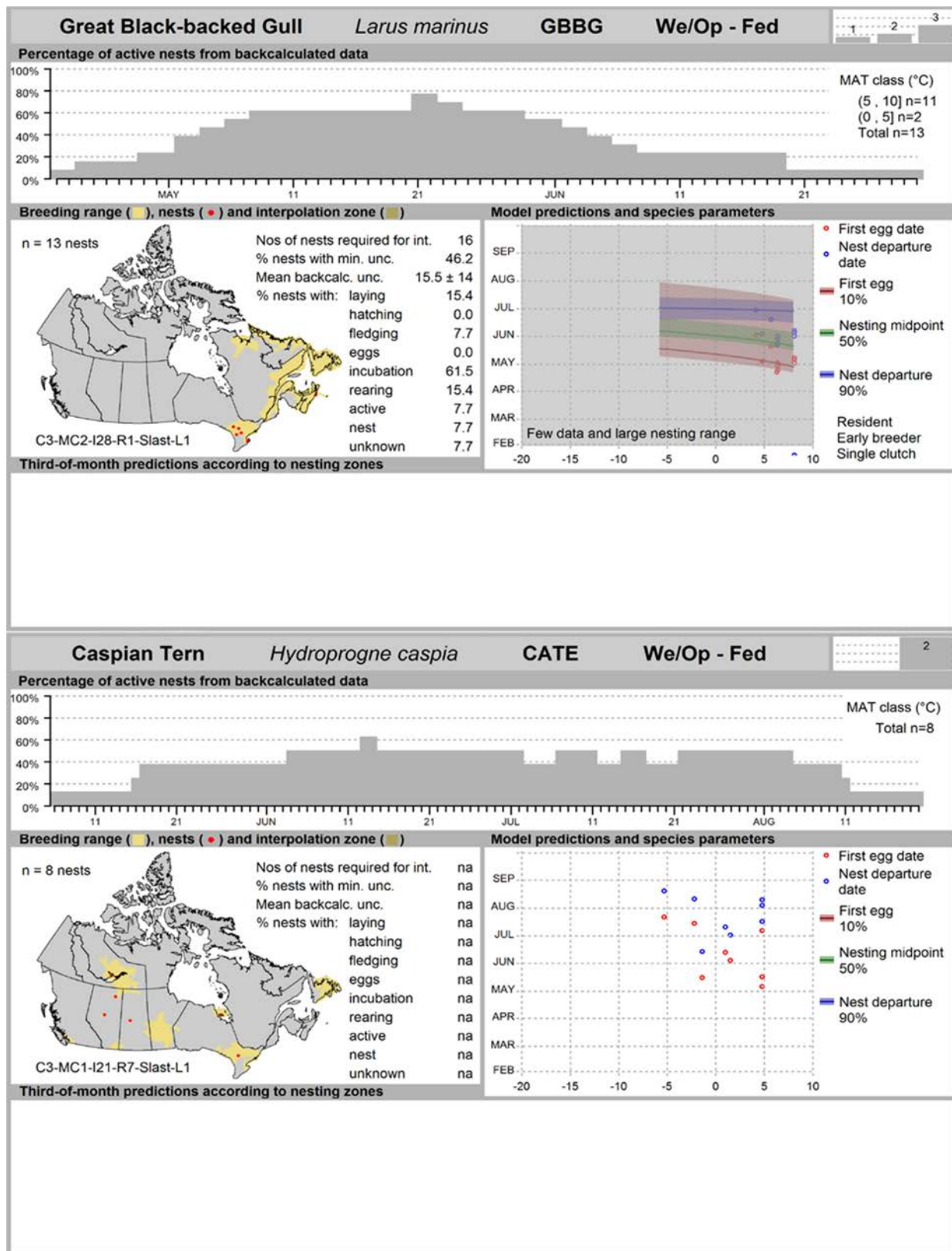












Caspian Tern

Hydroprogne caspia

CATE

We/Op - Fed

2

Percentage of active nests from backcalculated data

MAT class (°C)

Total n=8

Breeding range (), nests (•) and interpolation zone ()

n = 8 nests

Nos of nests required for int.

na

% nests with min. unc.

na

Mean backcalc. unc.

na

% nests with:

laying

na

hatching

na

fledging

na

eggs

na

incubation

na

rearing

na

active

na

nest

na

unknown

na

C3-MC1-I21-R7-Slast-L1

Model predictions and species parameters

• First egg date

• Nest departure date

— First egg 10%

— Nesting midpoint 50%

— Nest departure 90%

SEP

AUG

JUL

JUN

MAY

APR

MAR

FEB

-20

-15

-10

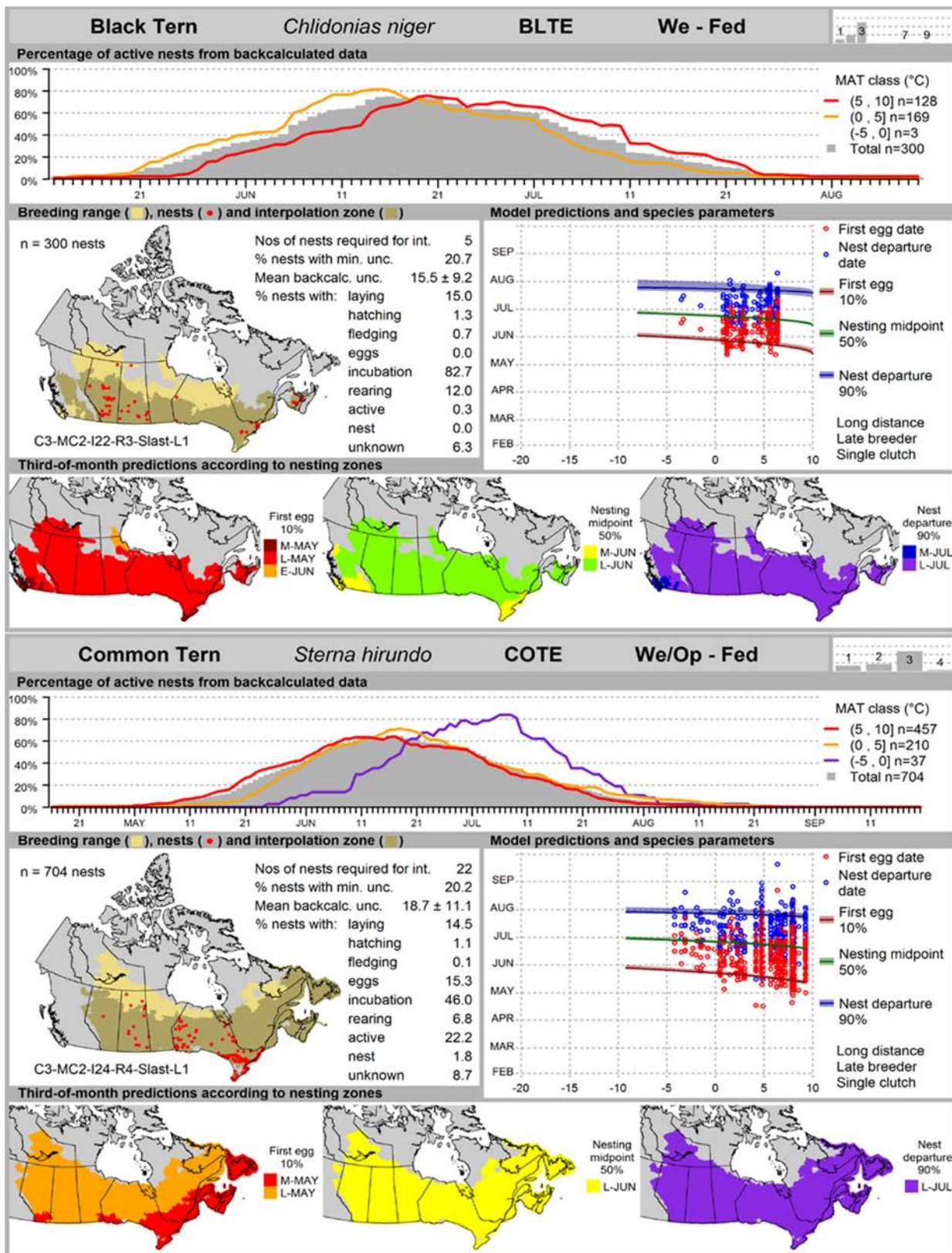
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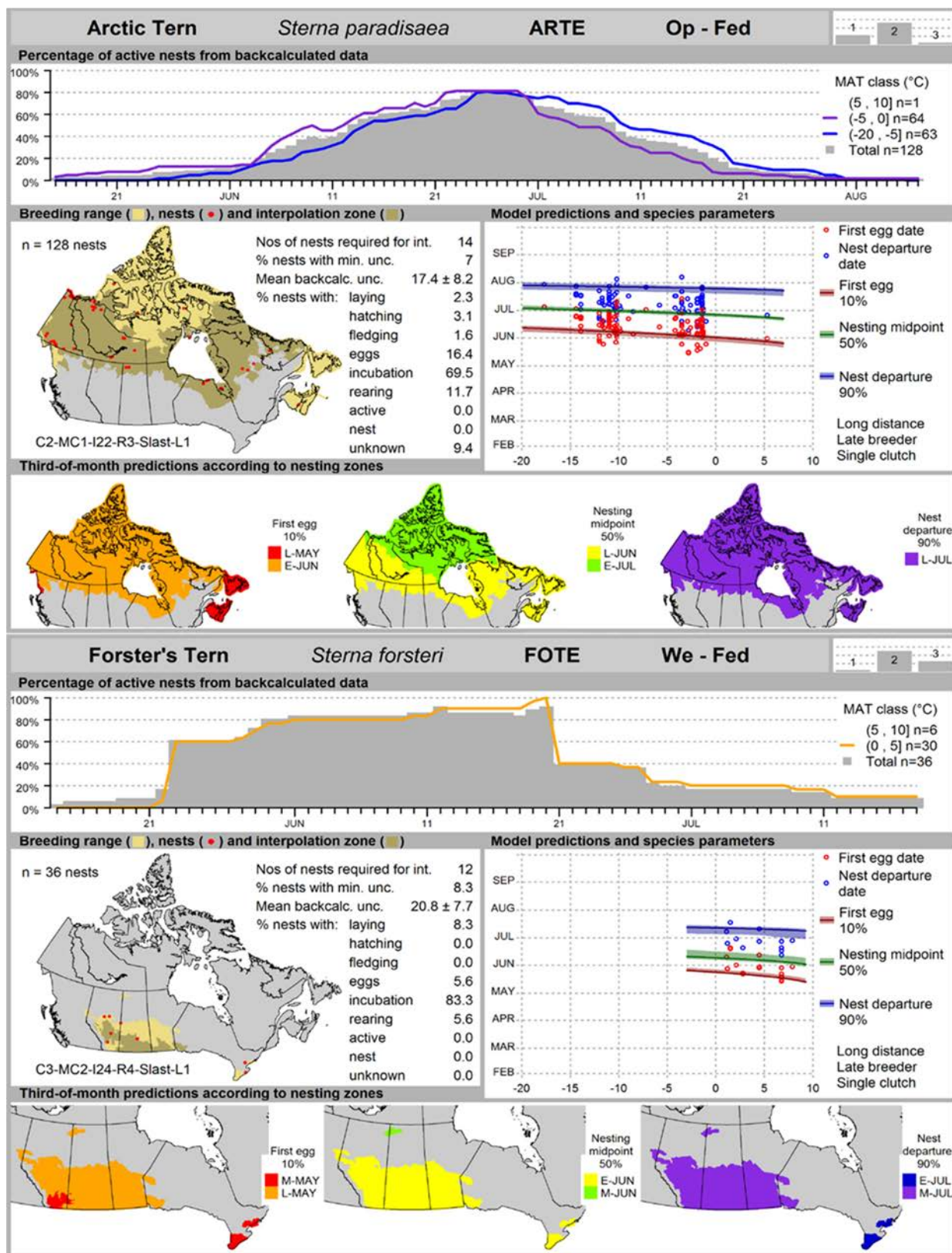
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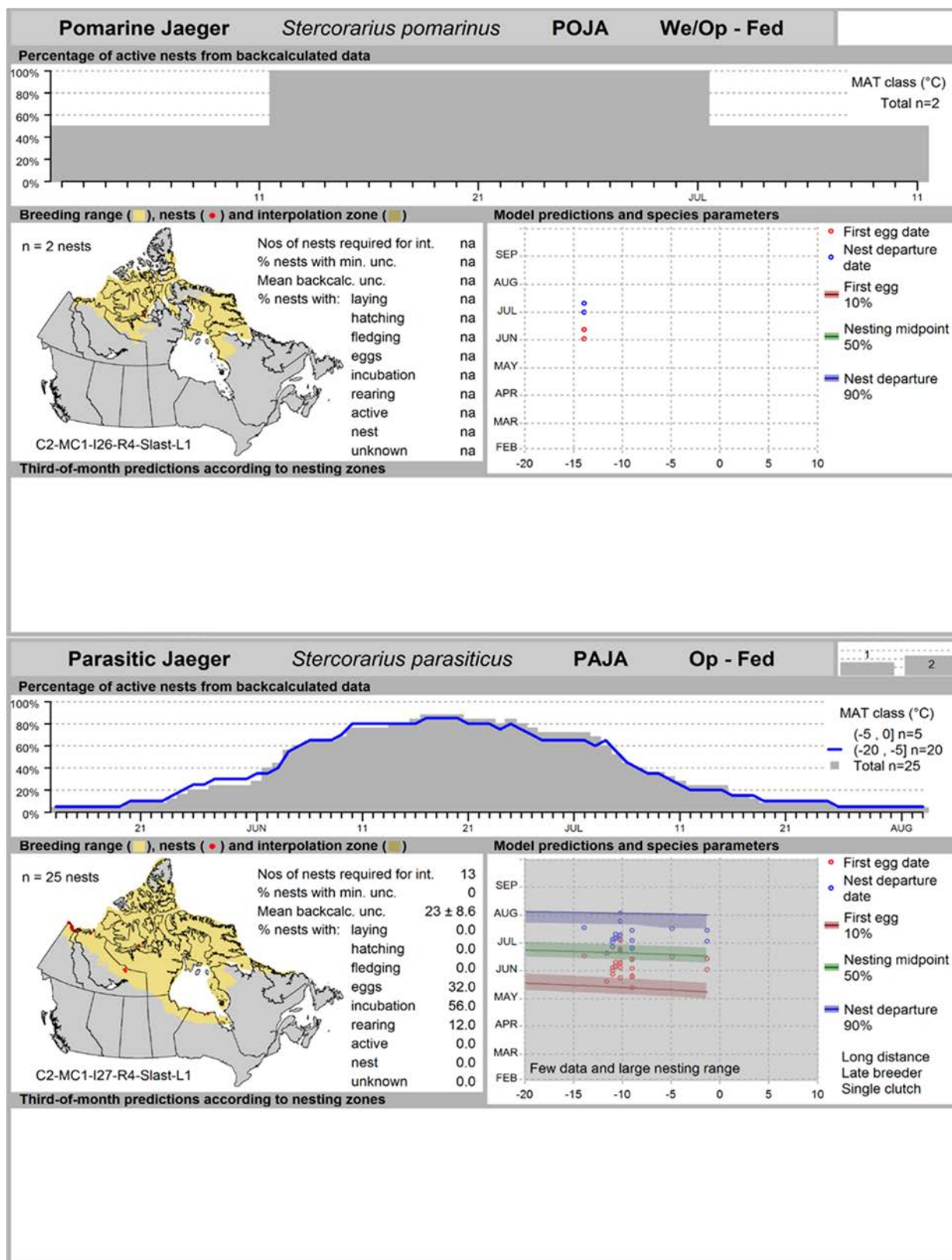
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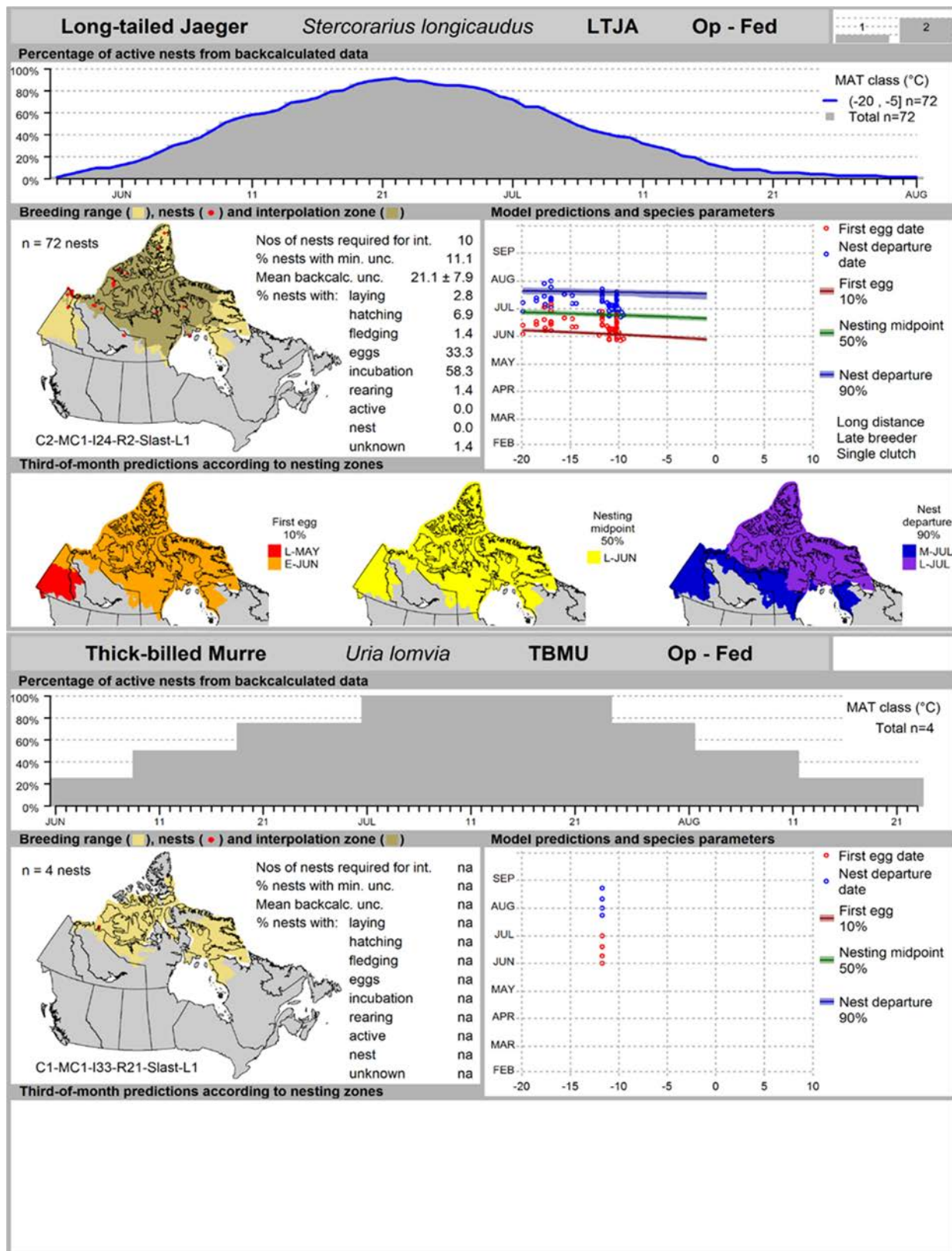
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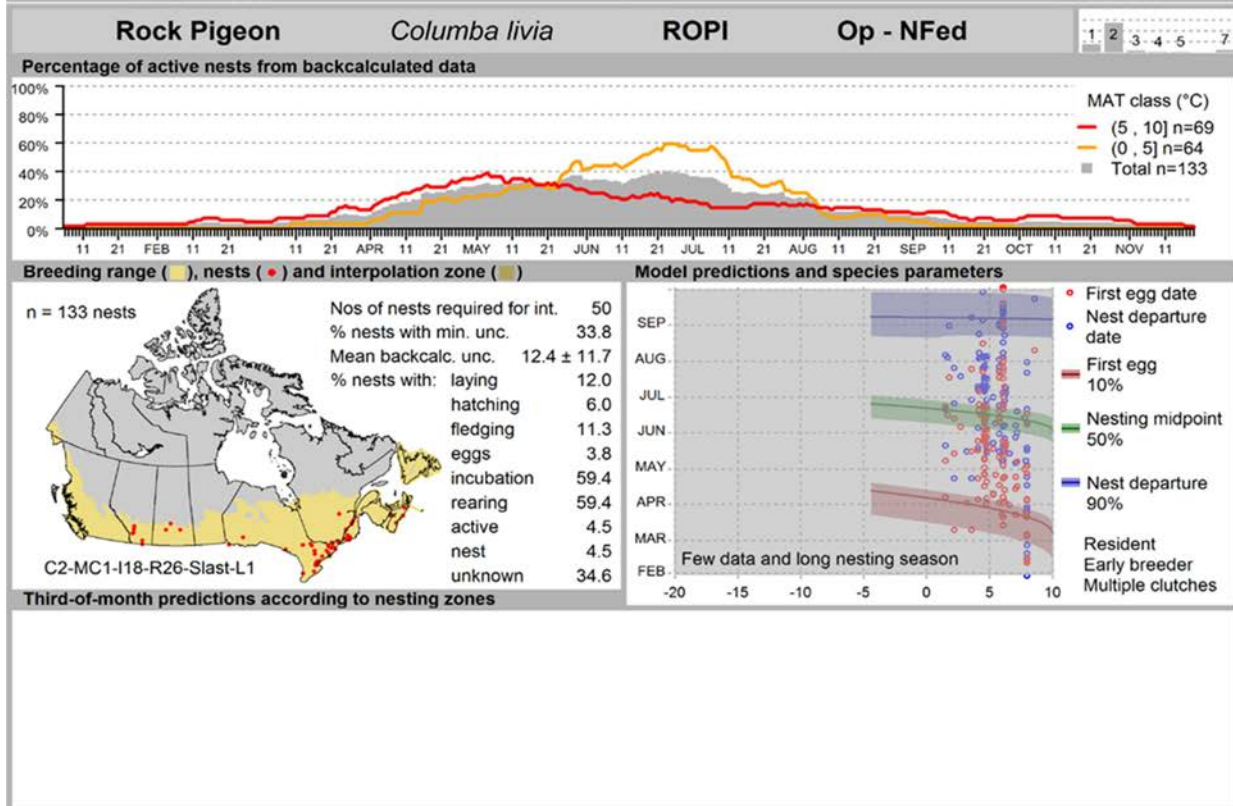
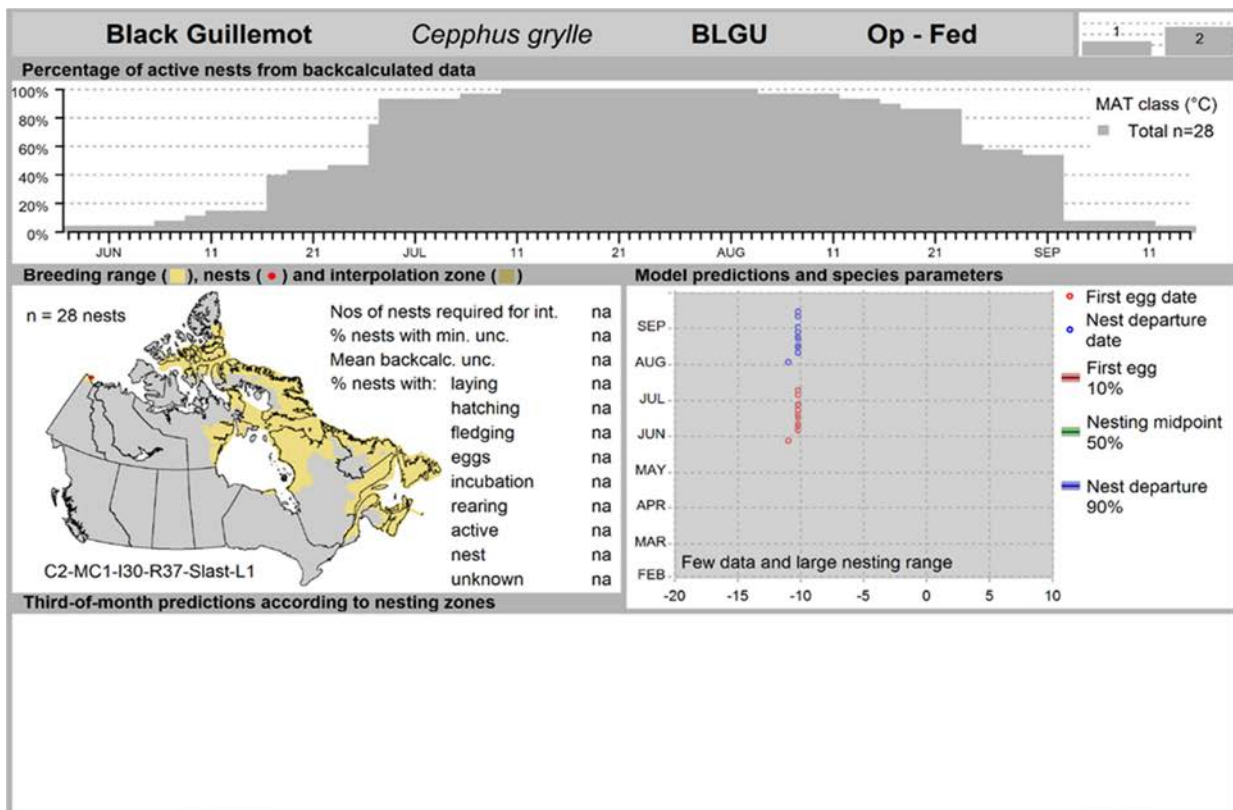
Third-of-month predictions according to nesting zones

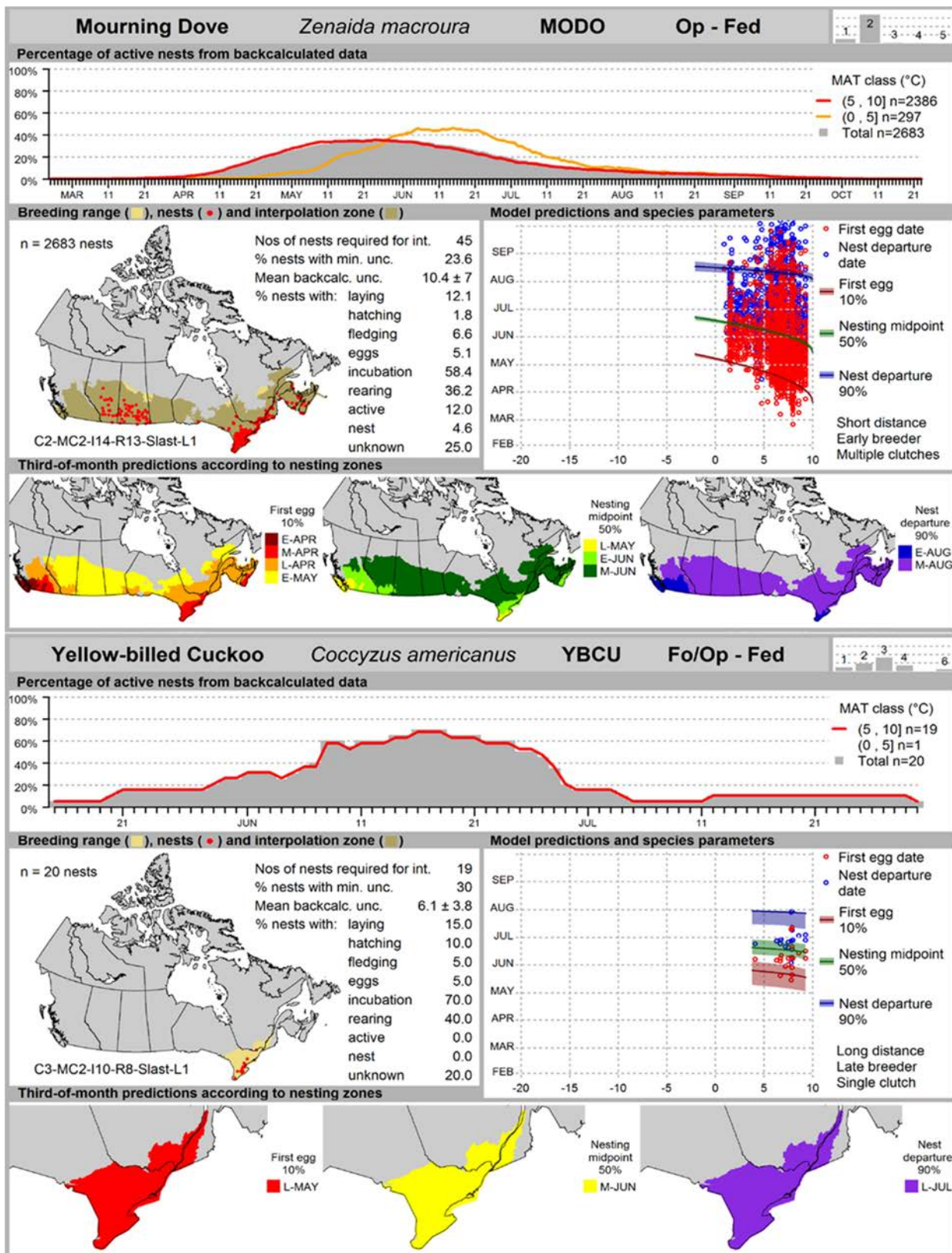


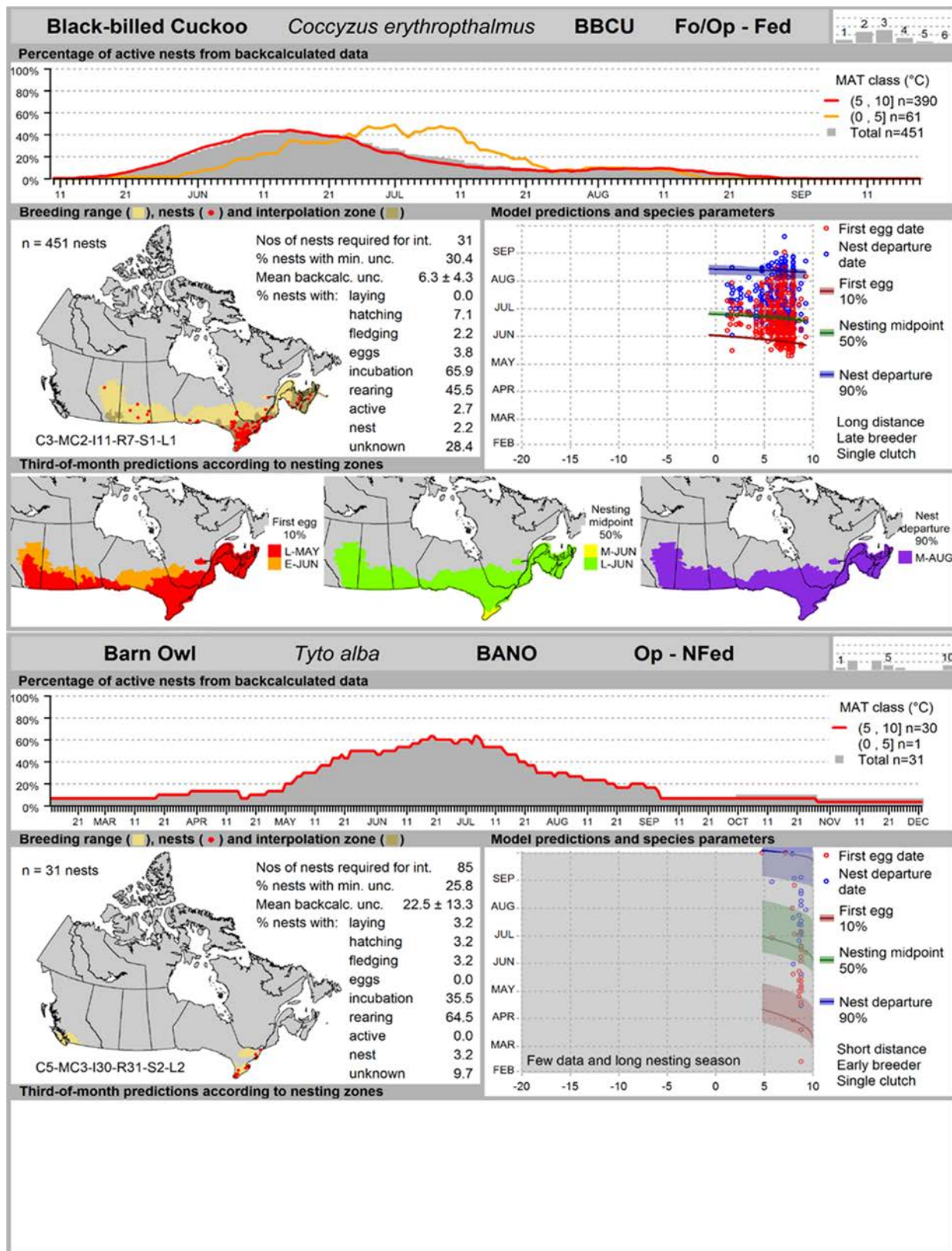


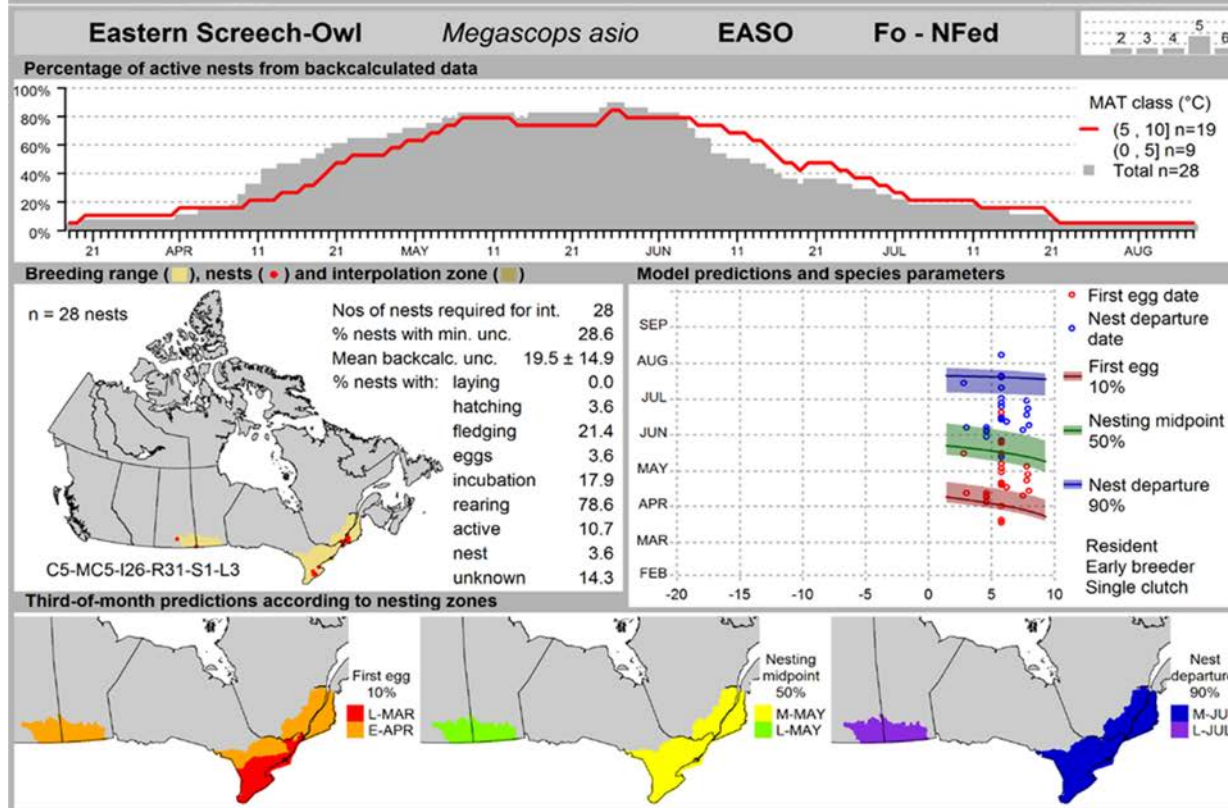
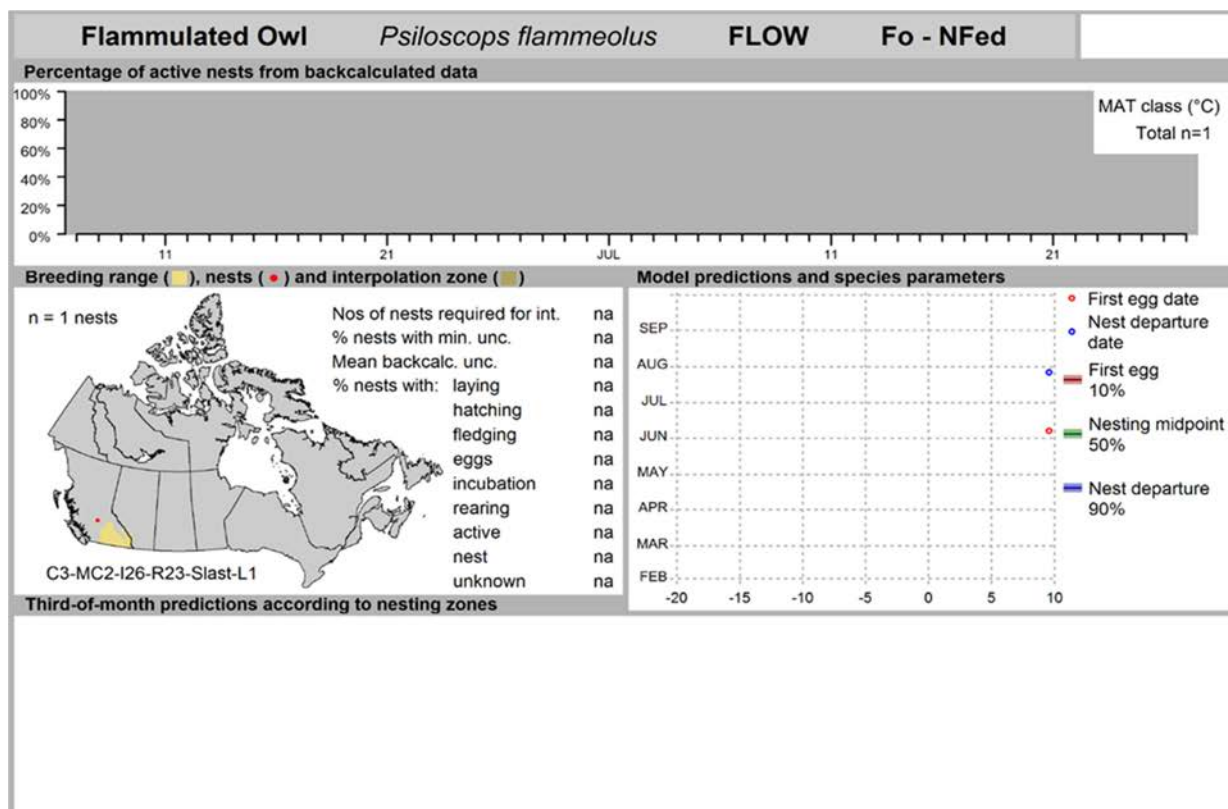


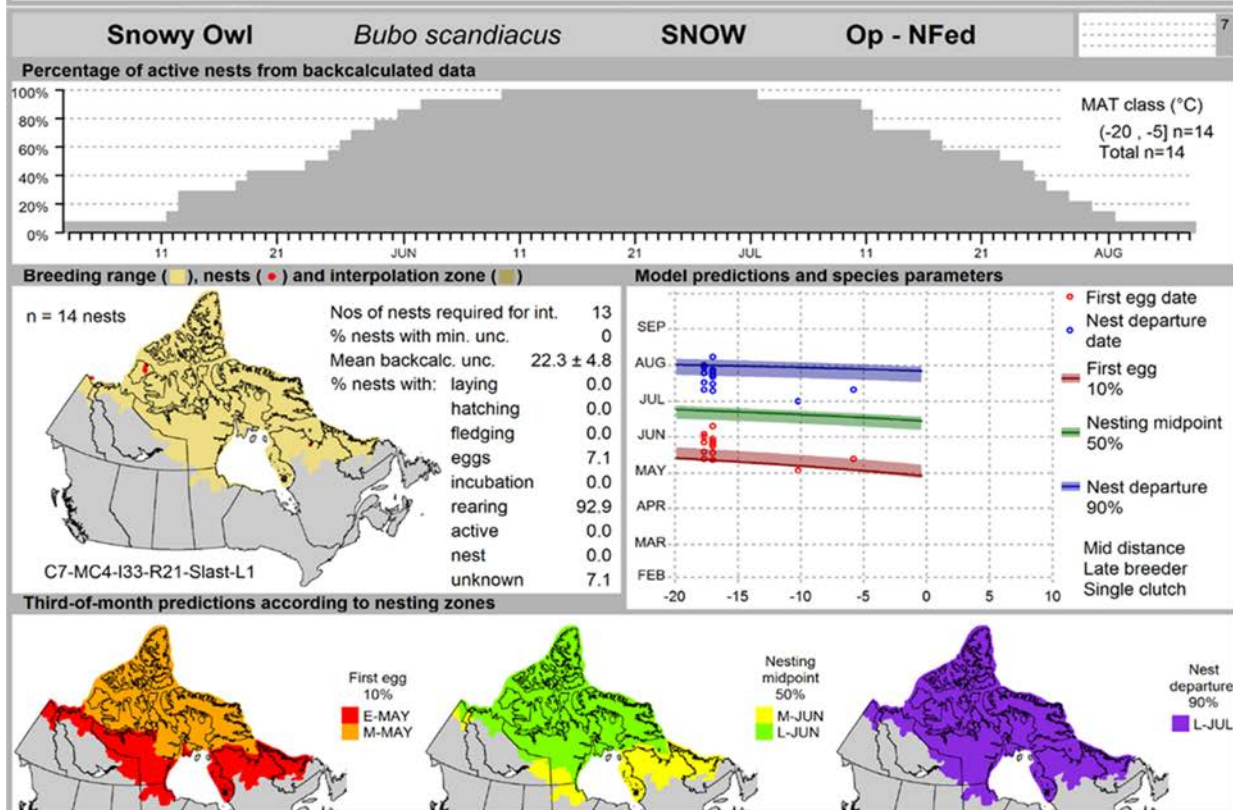
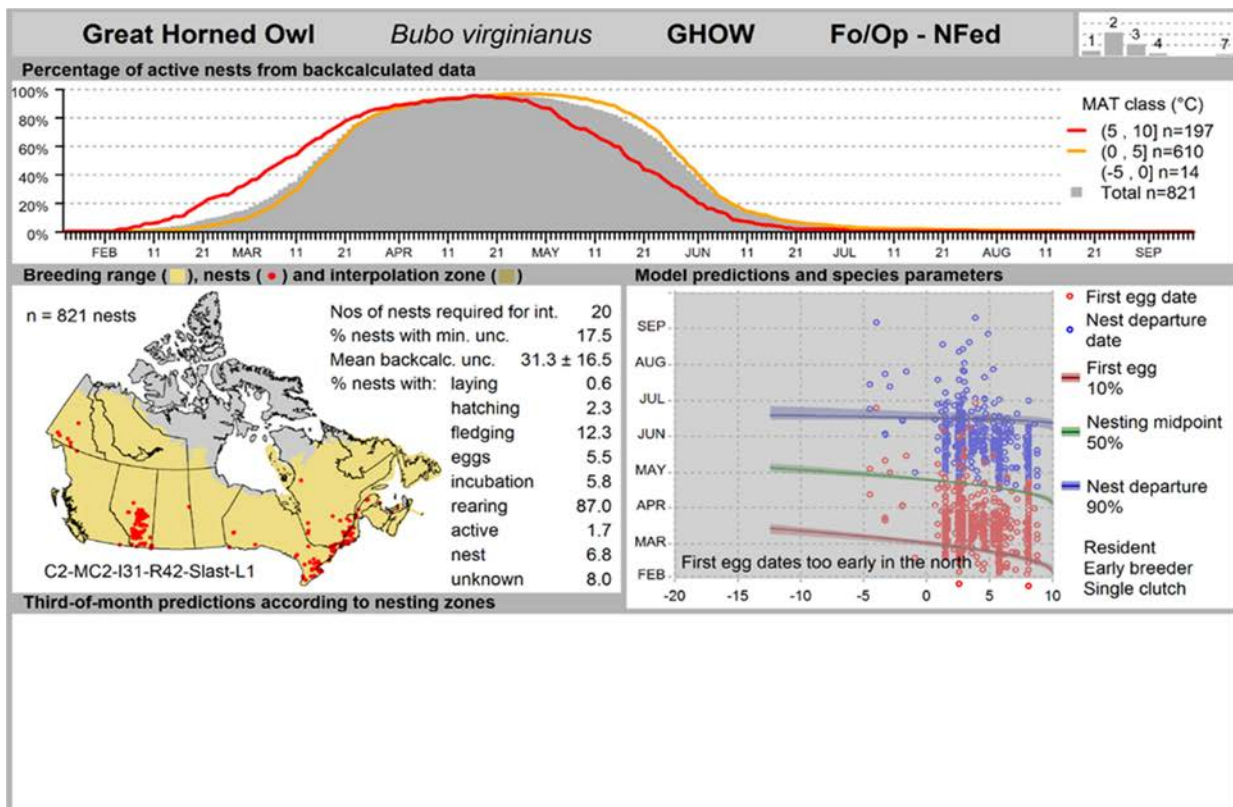


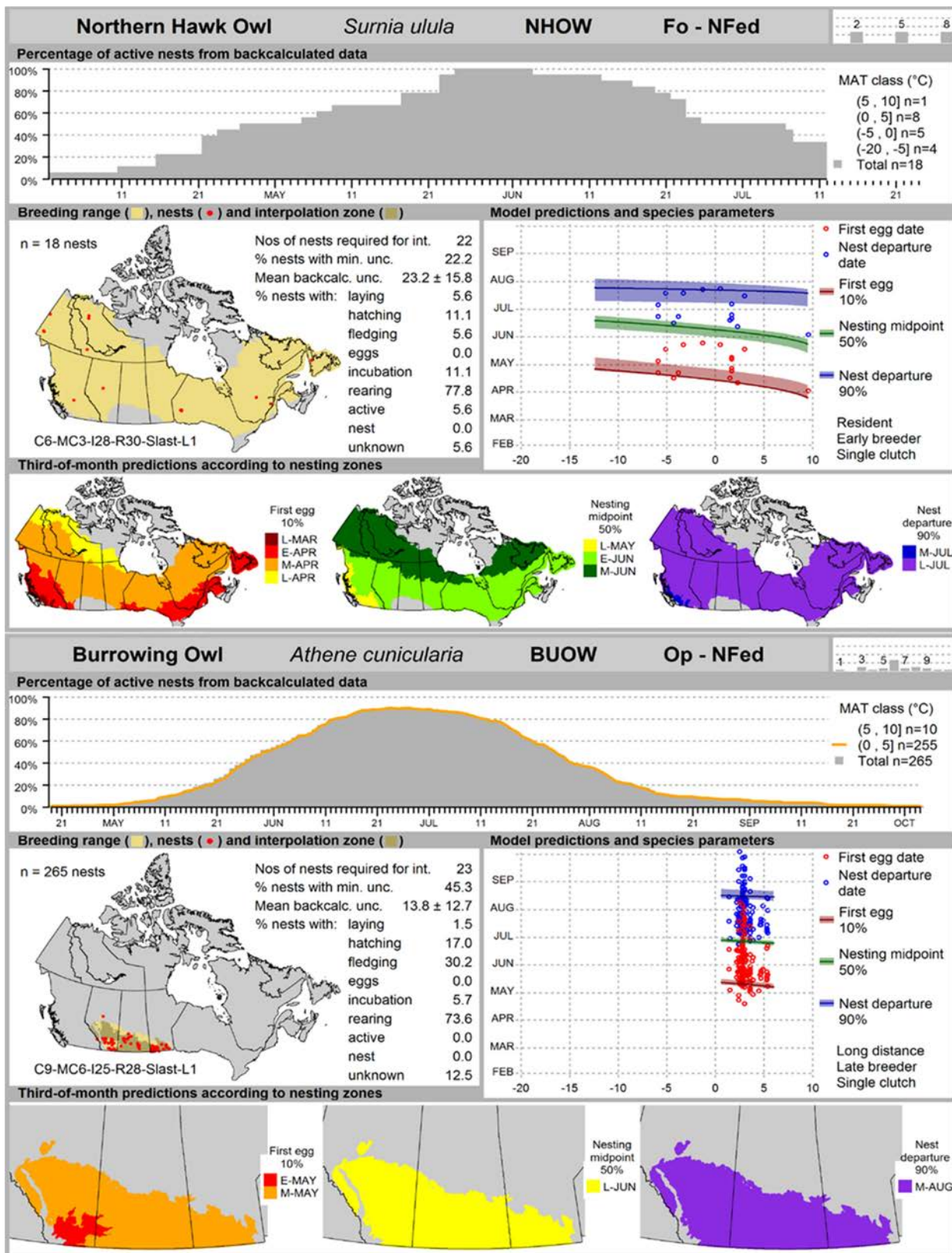


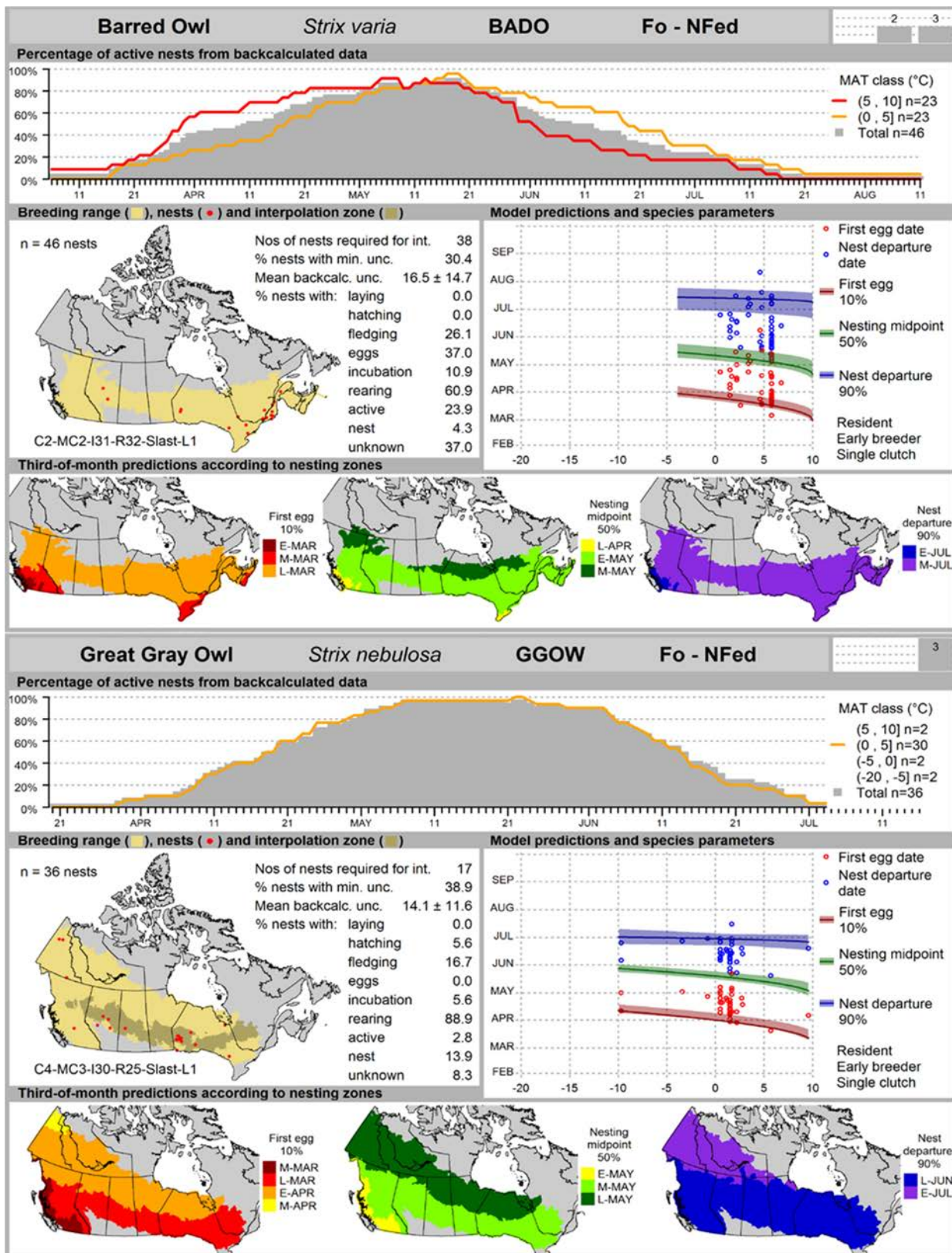


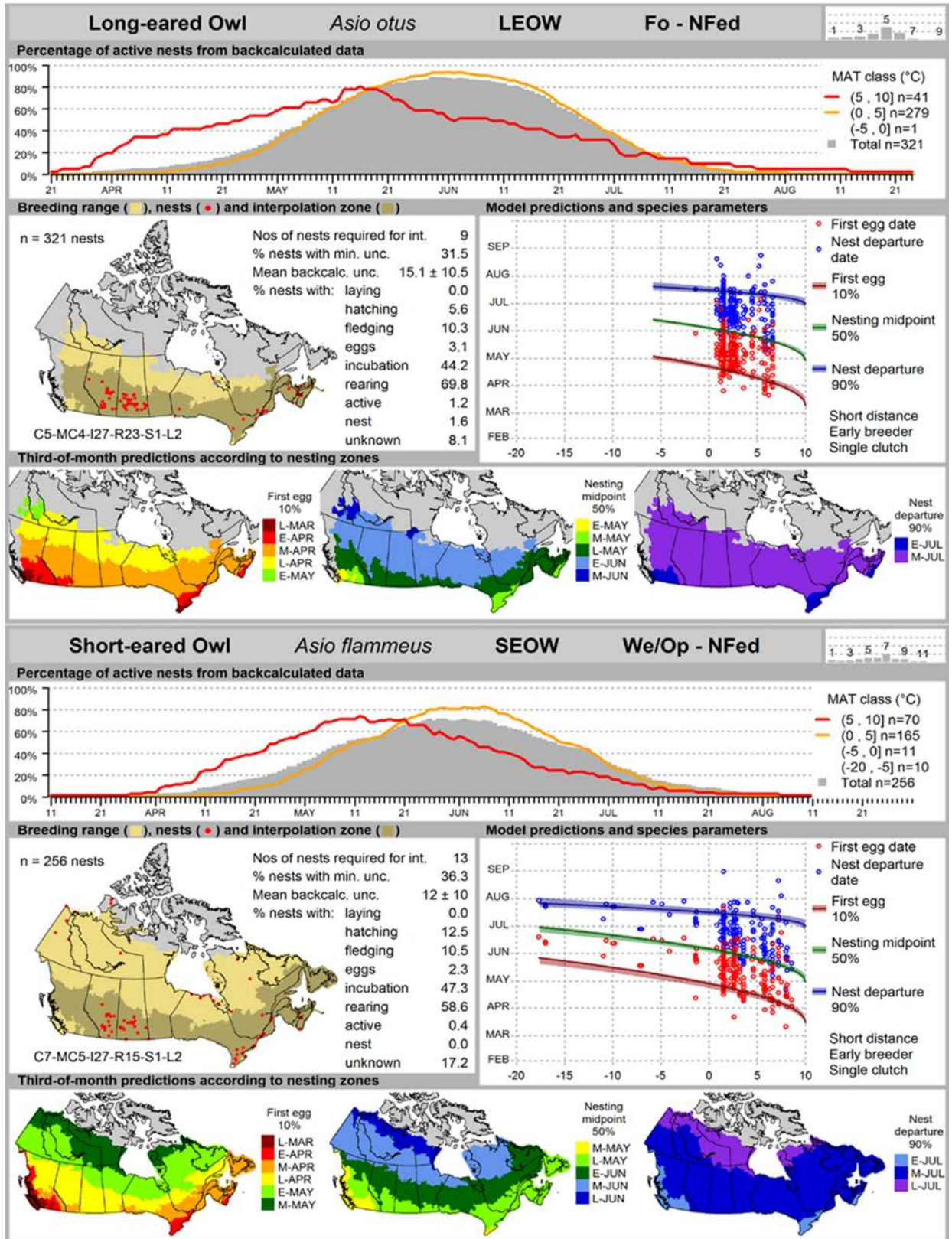


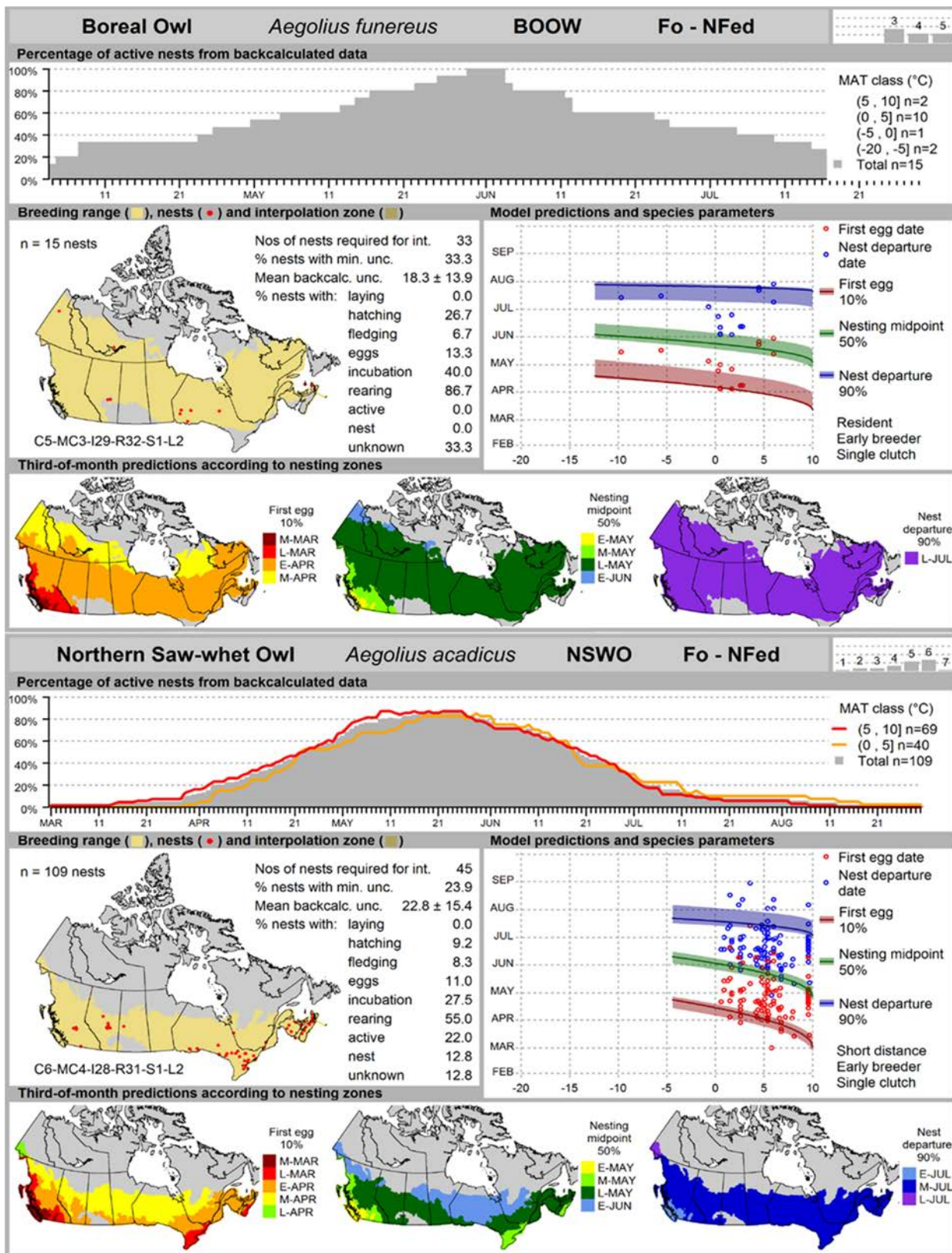


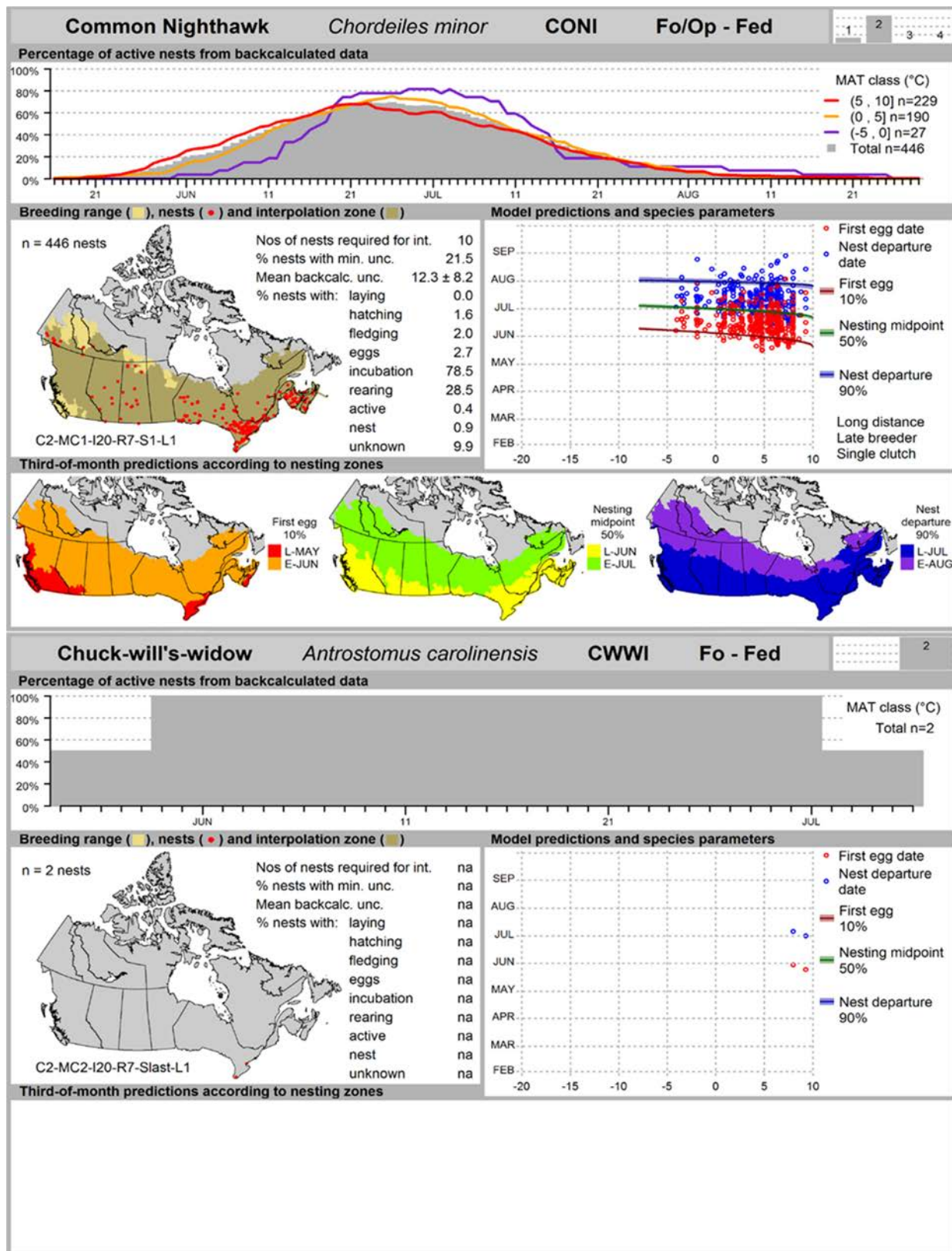


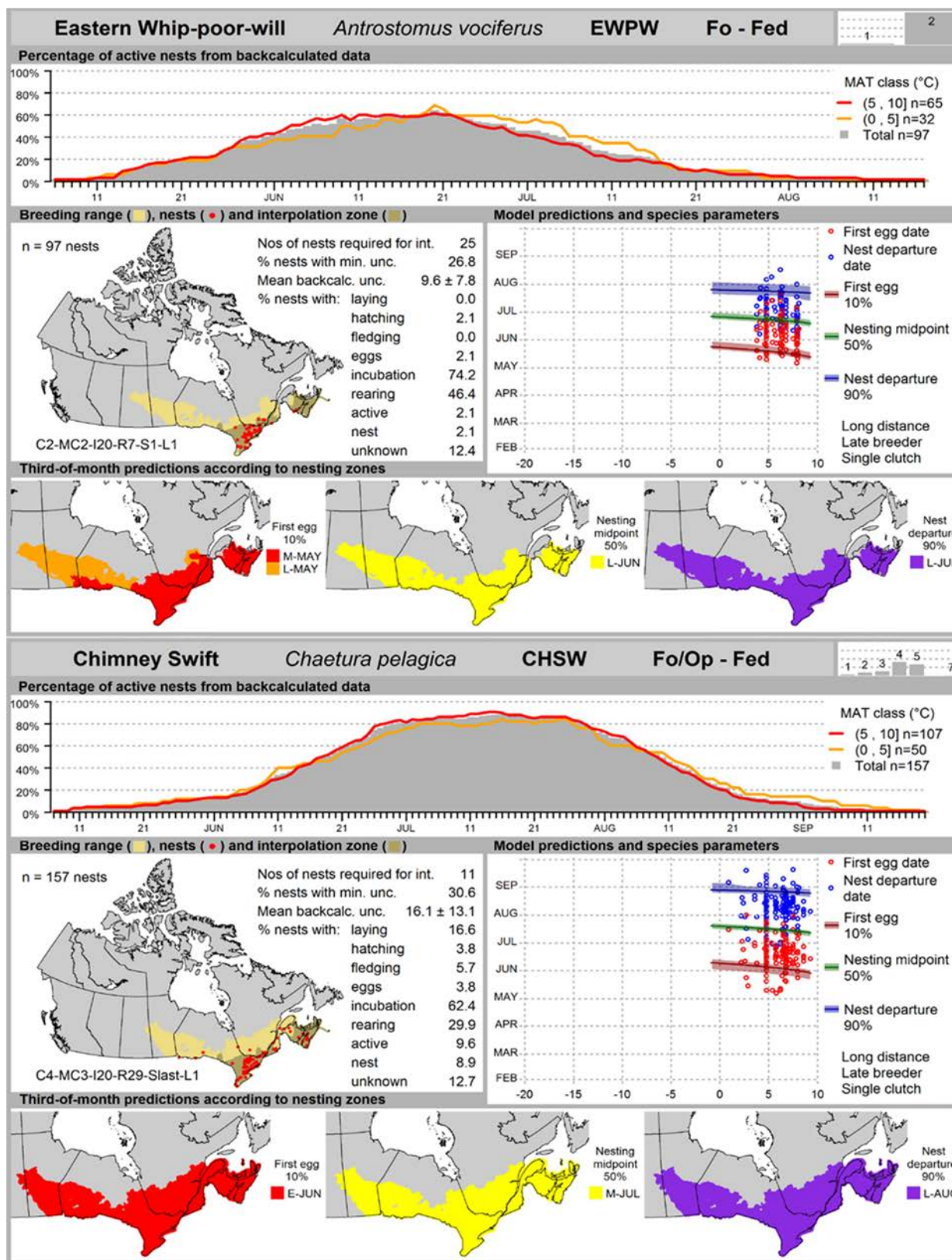


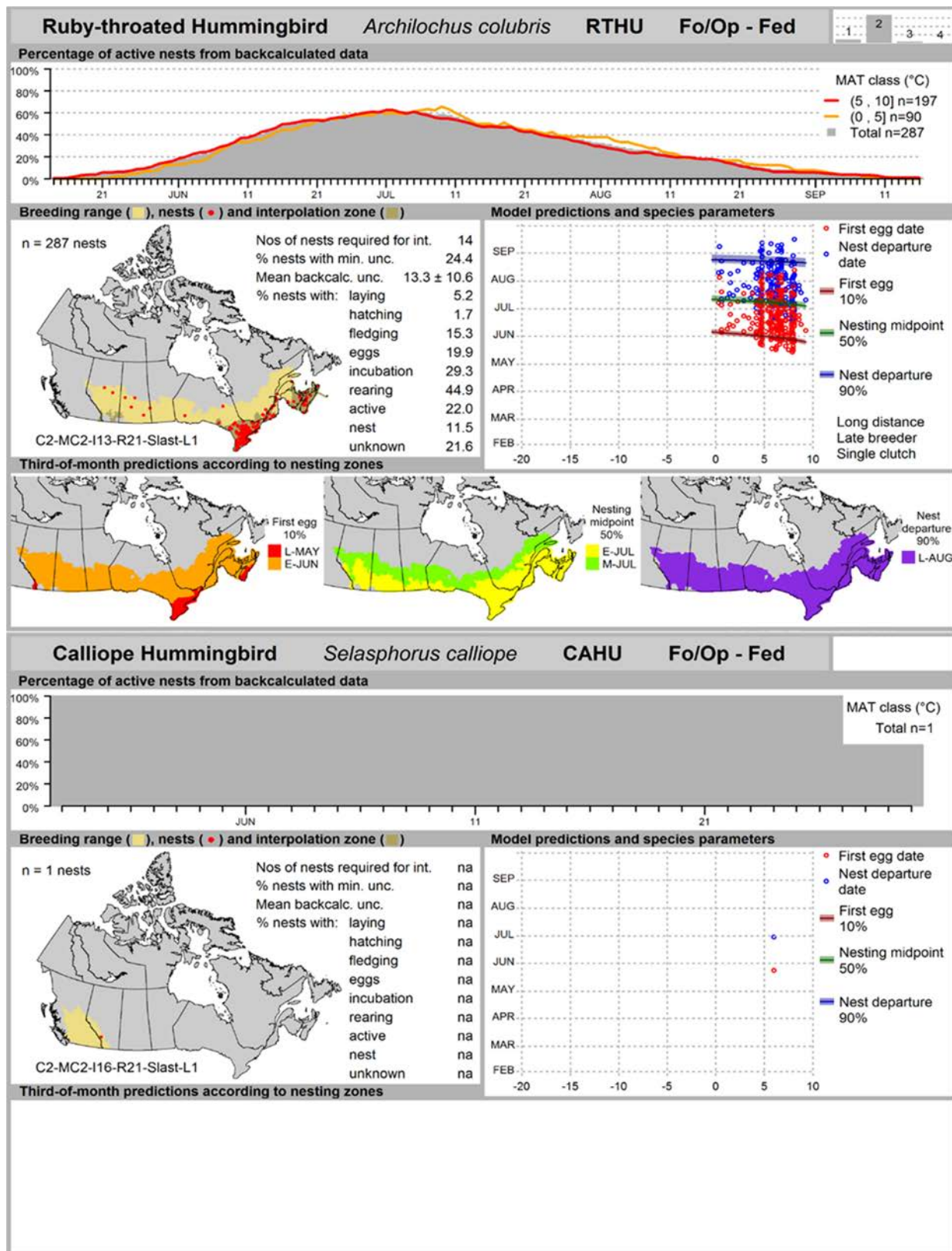


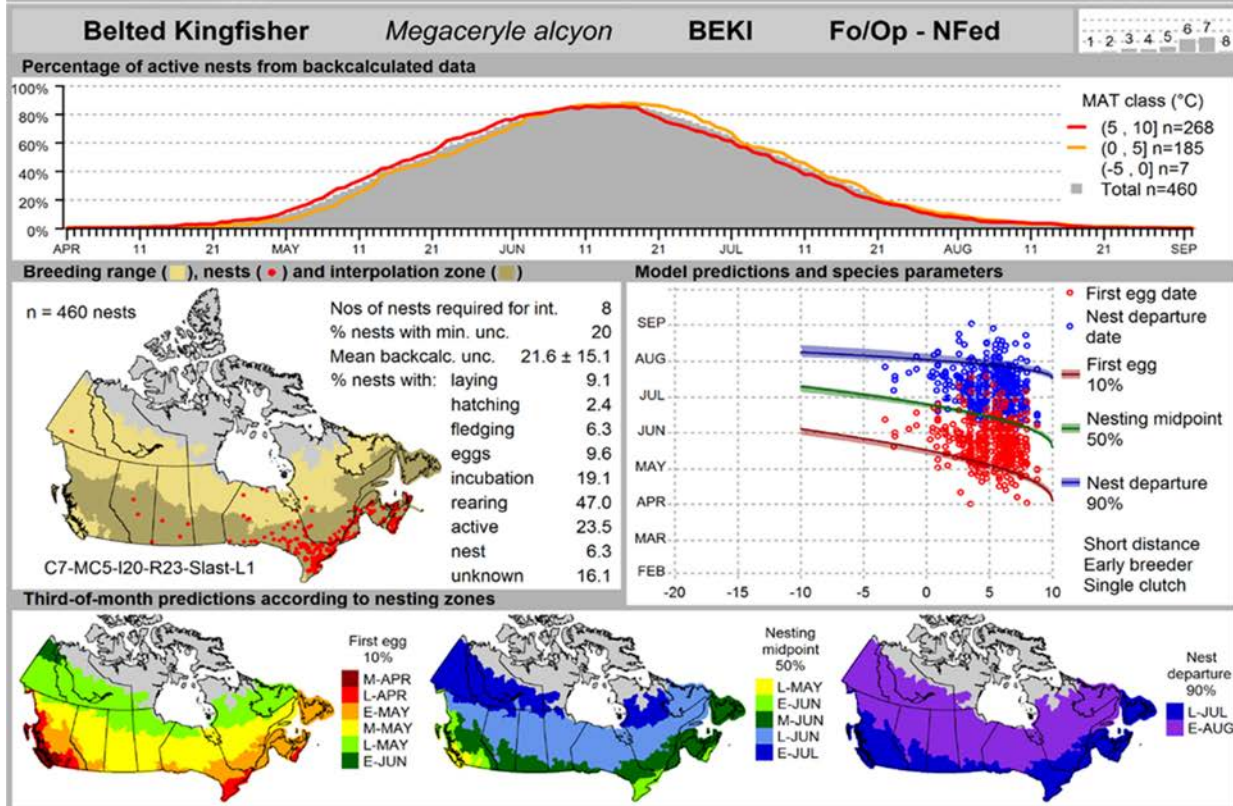
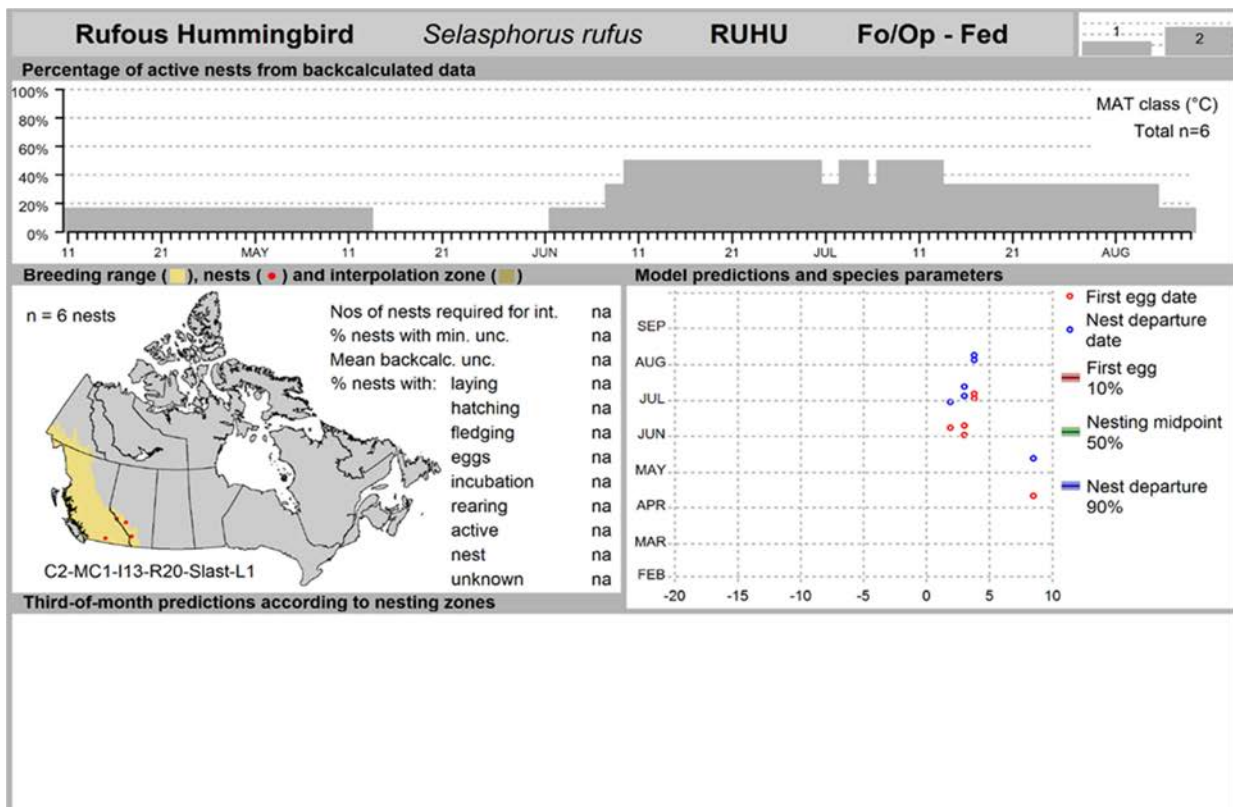


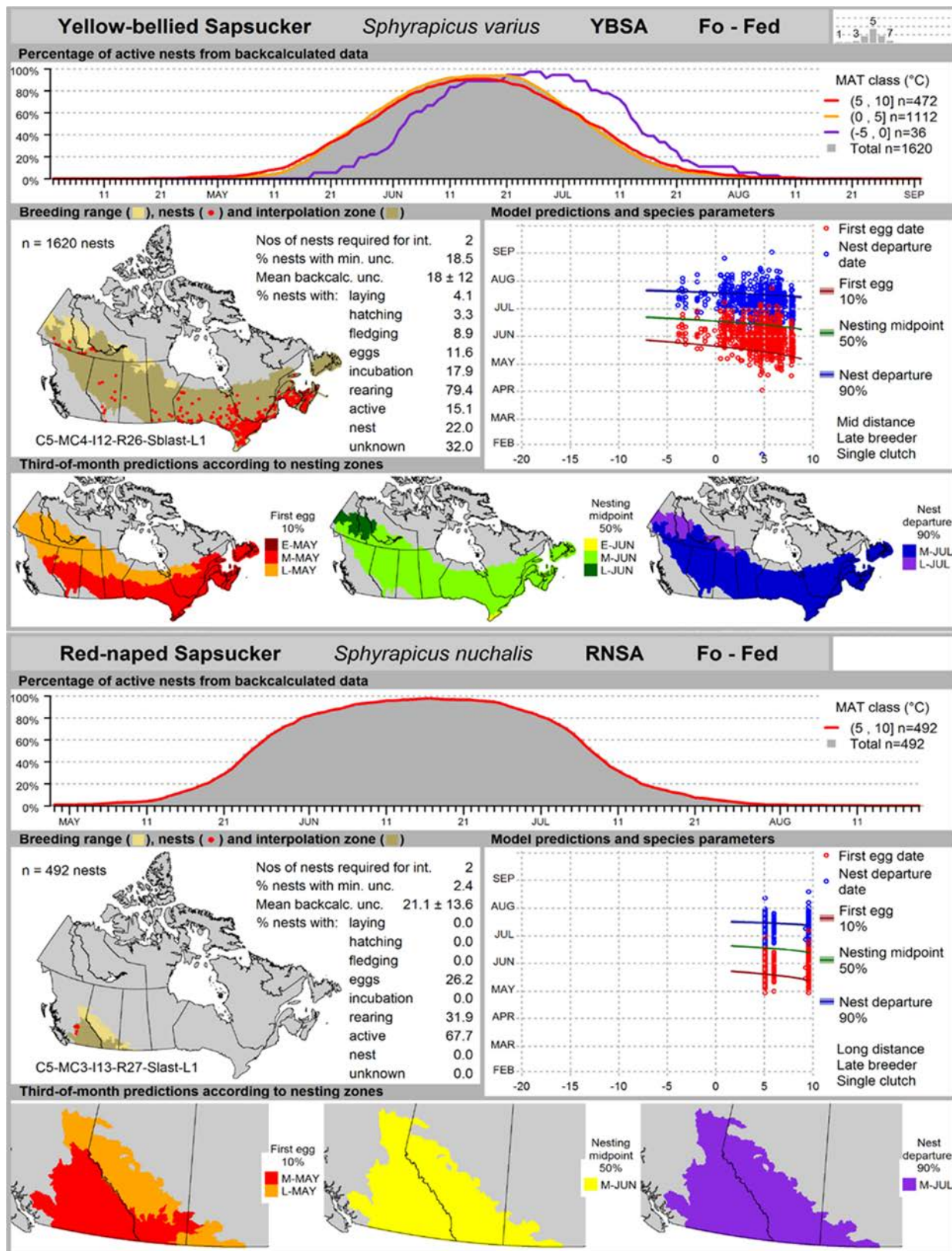


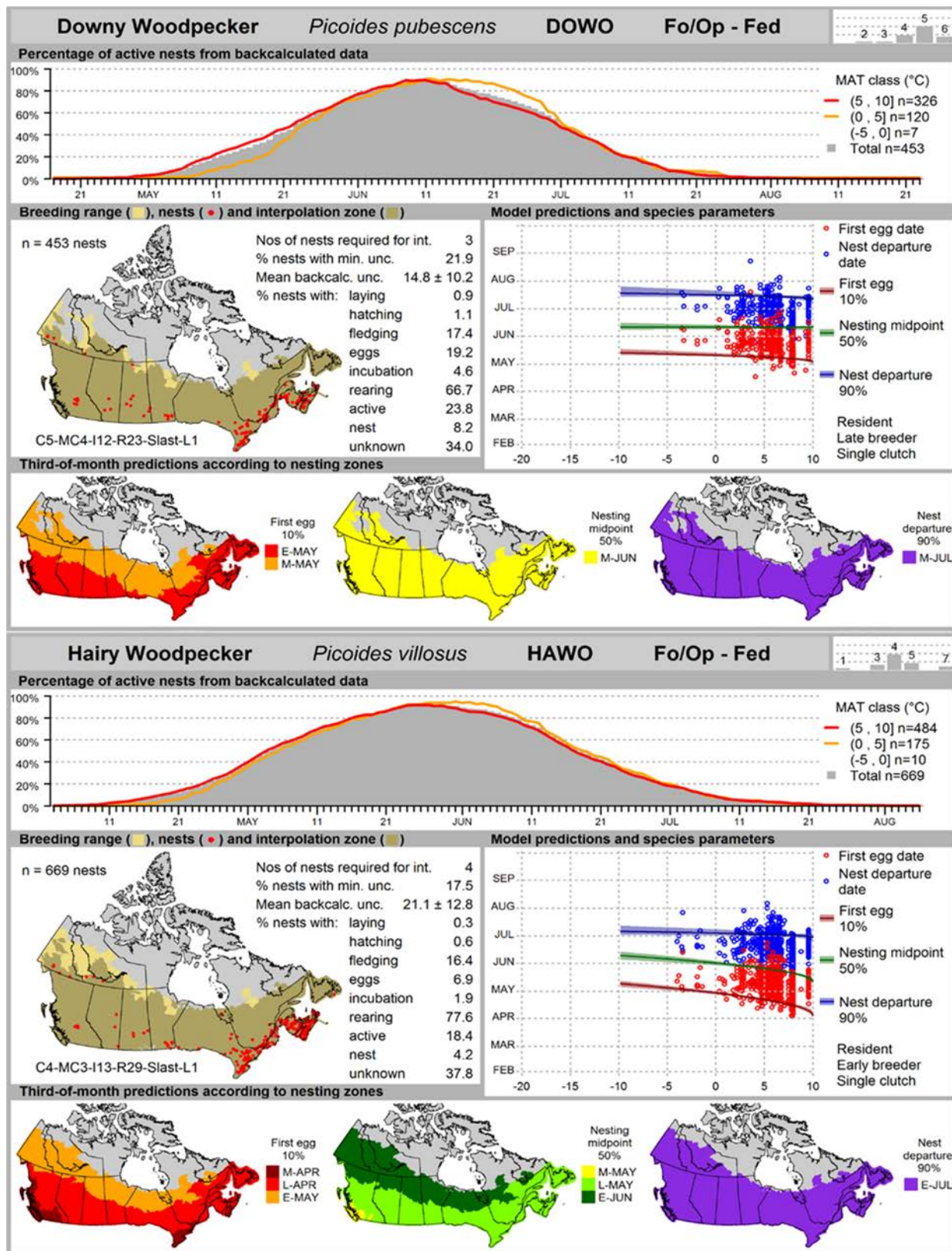


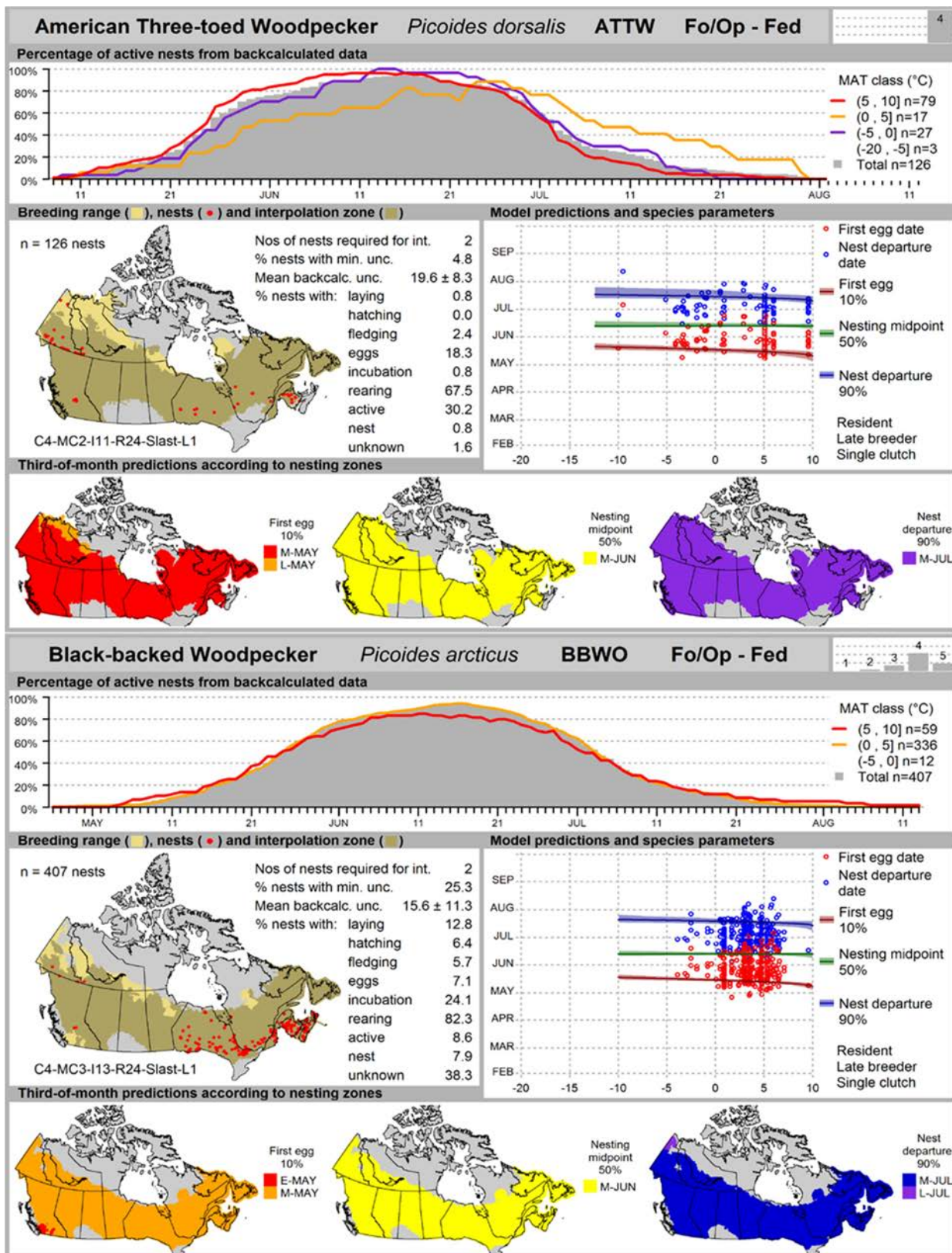


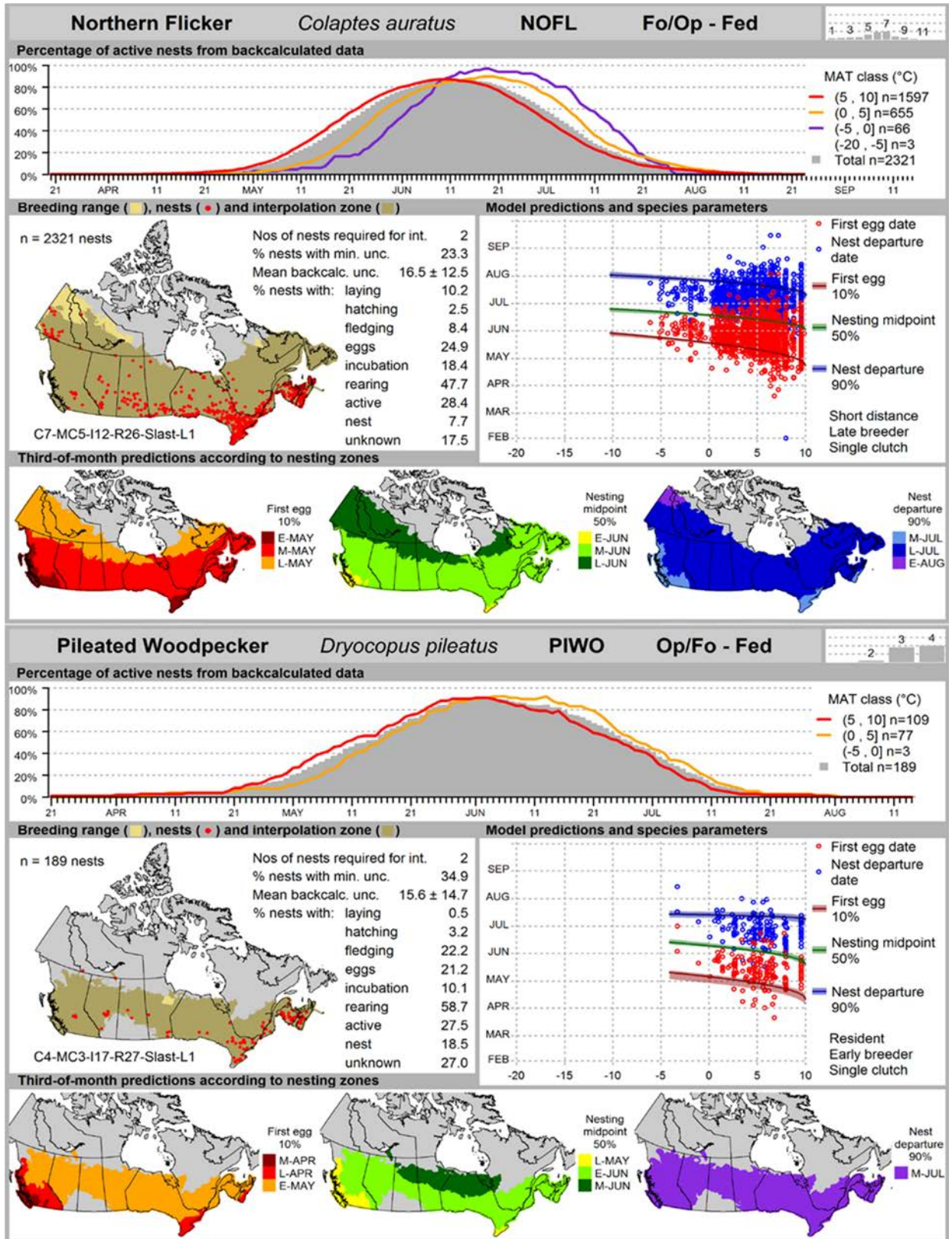


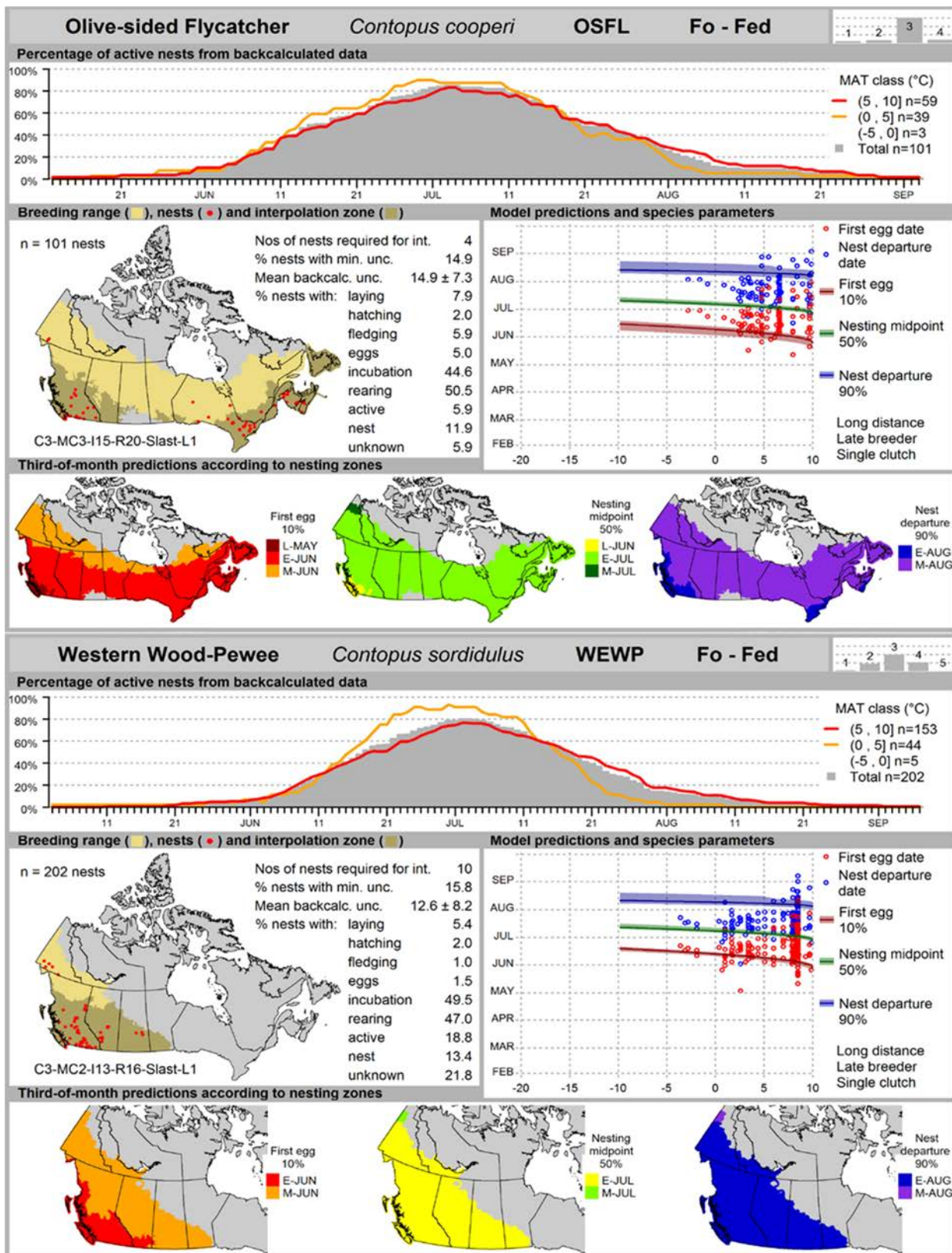


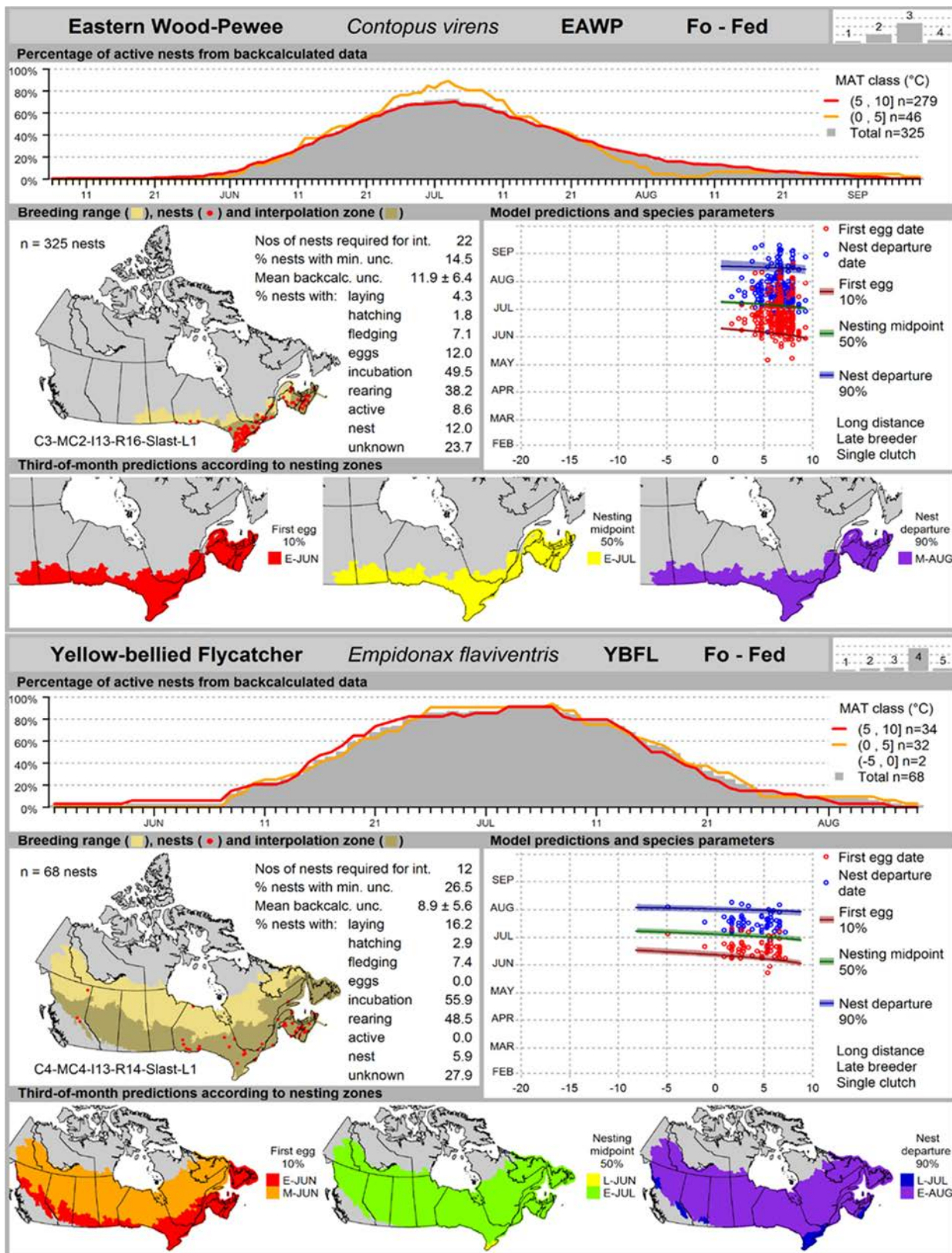


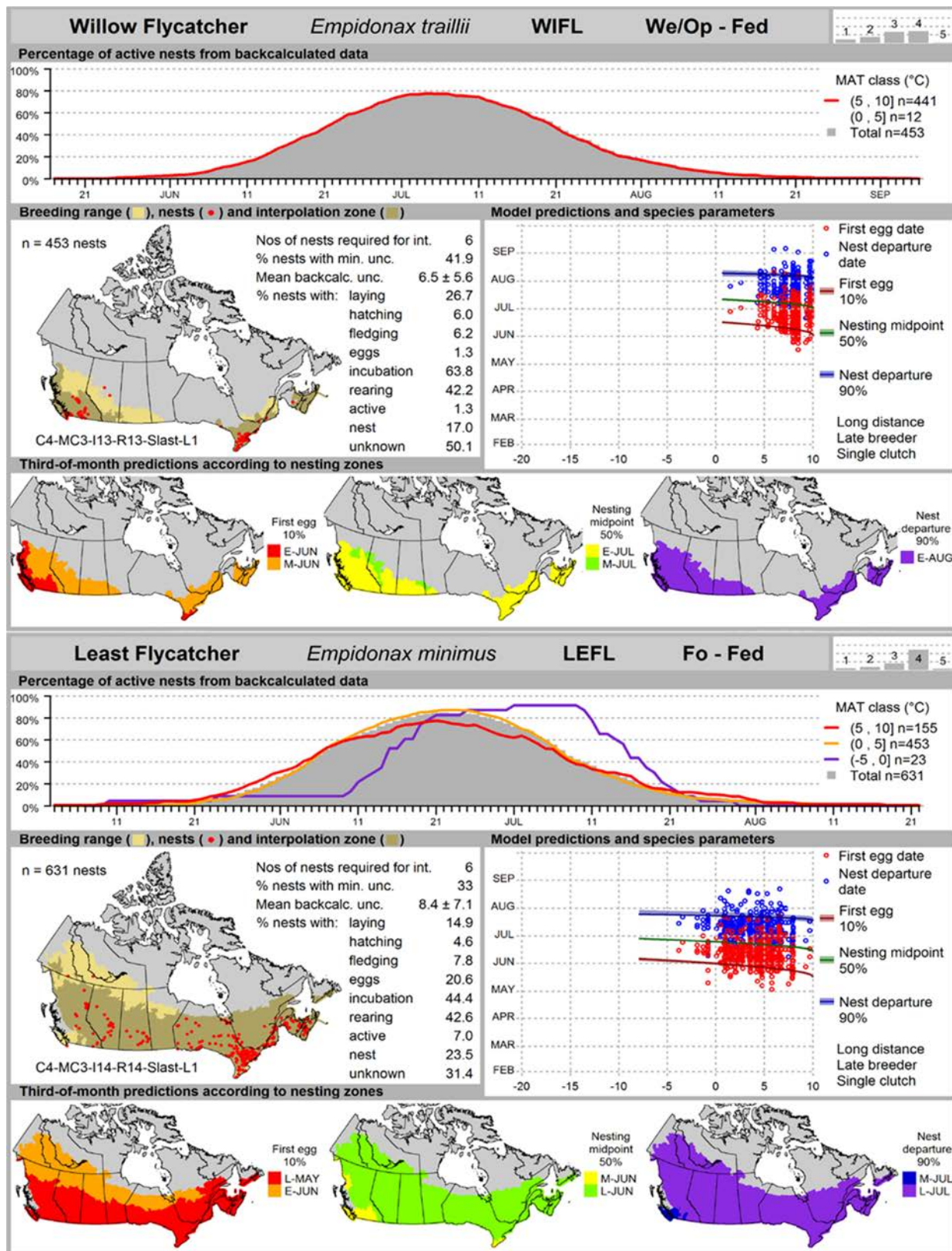


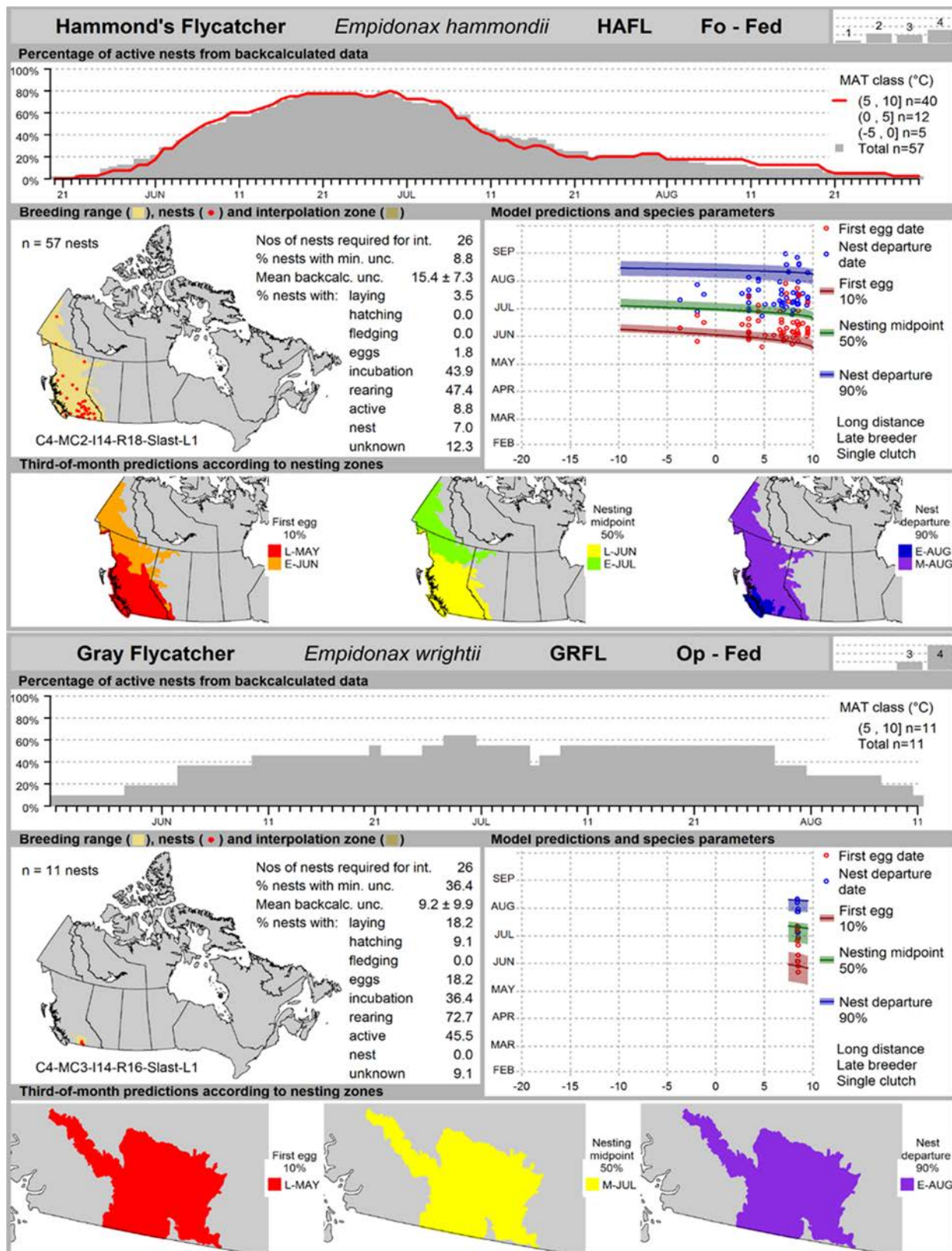


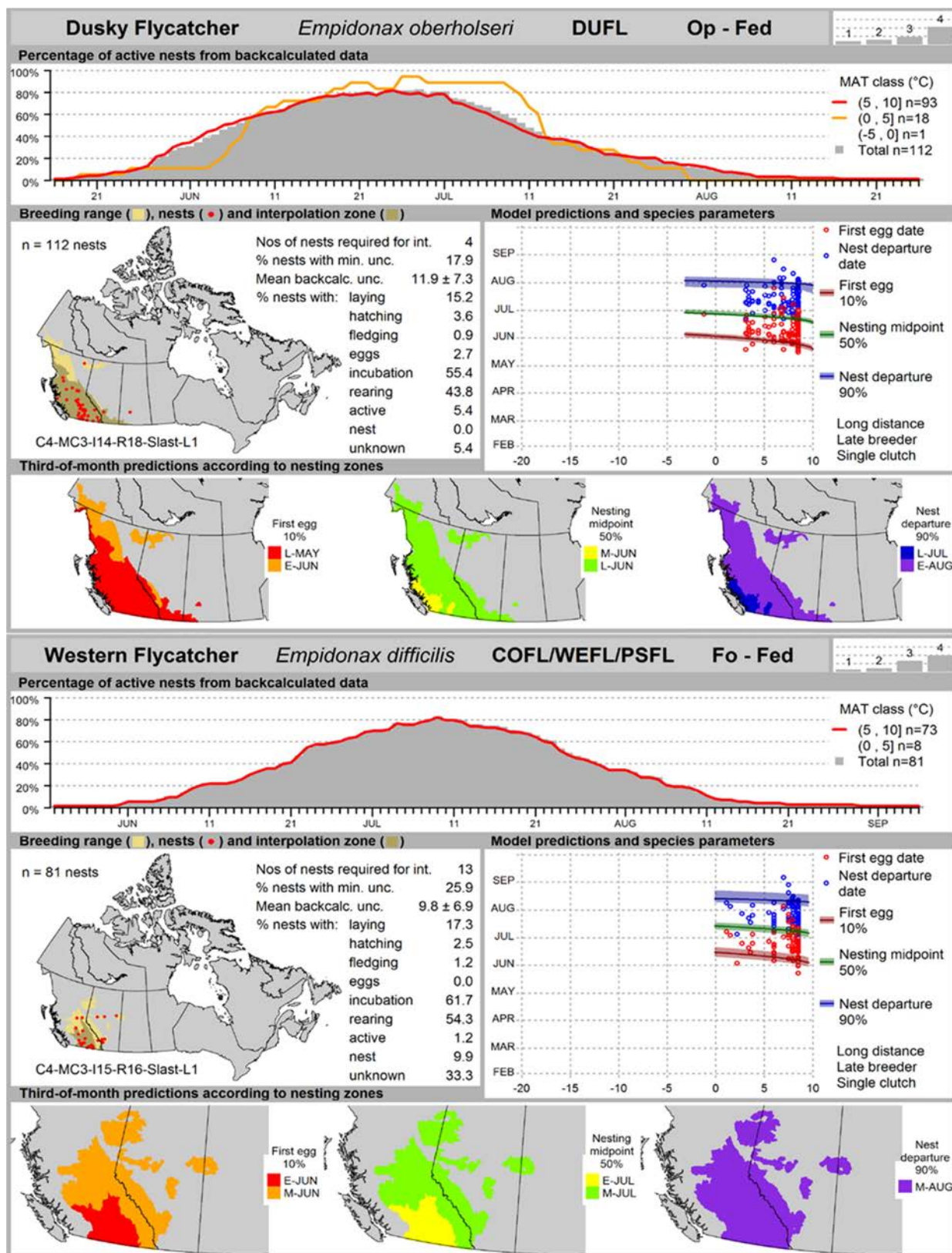


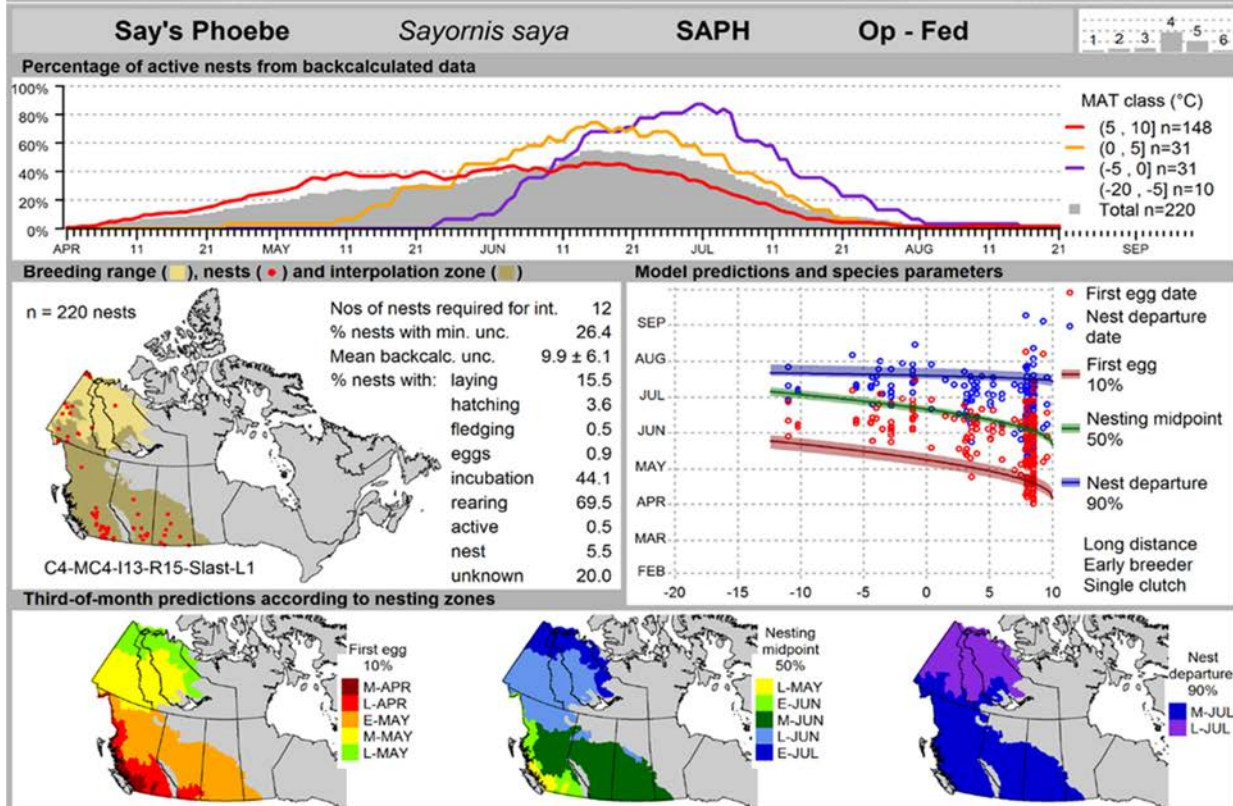
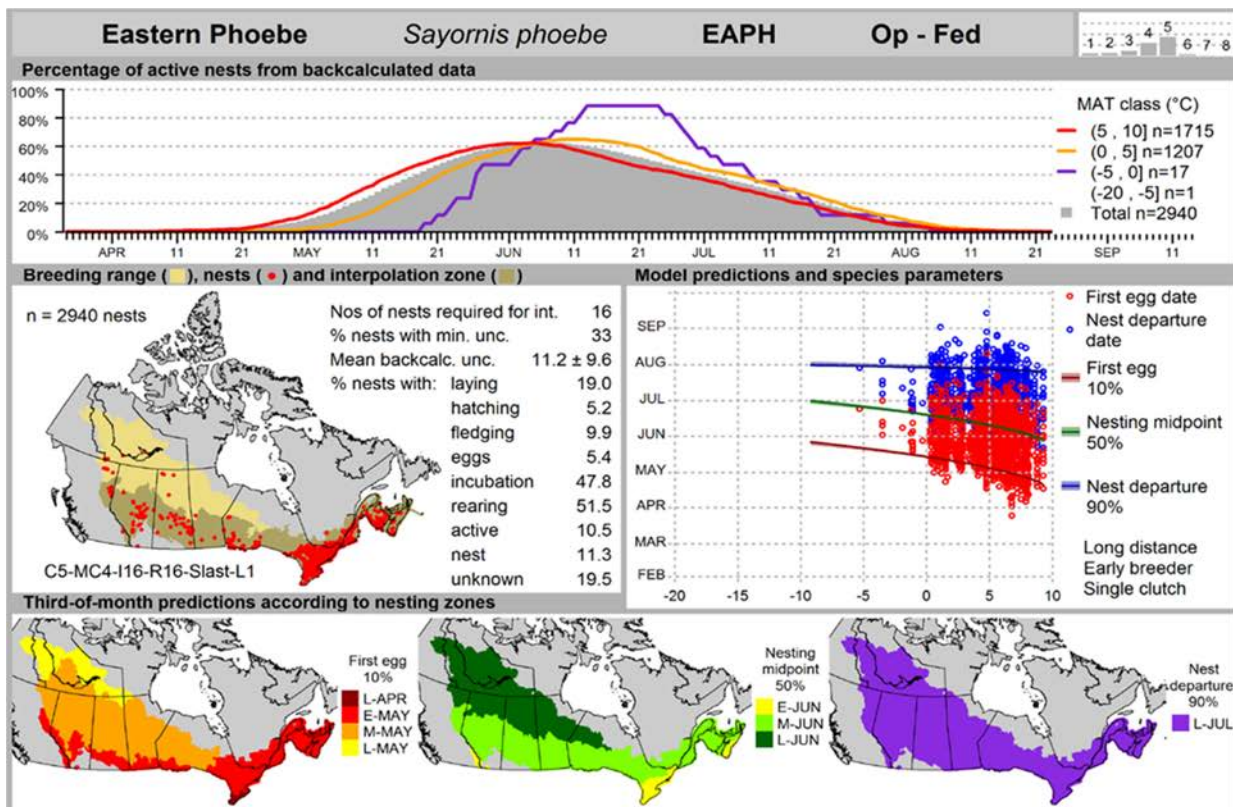


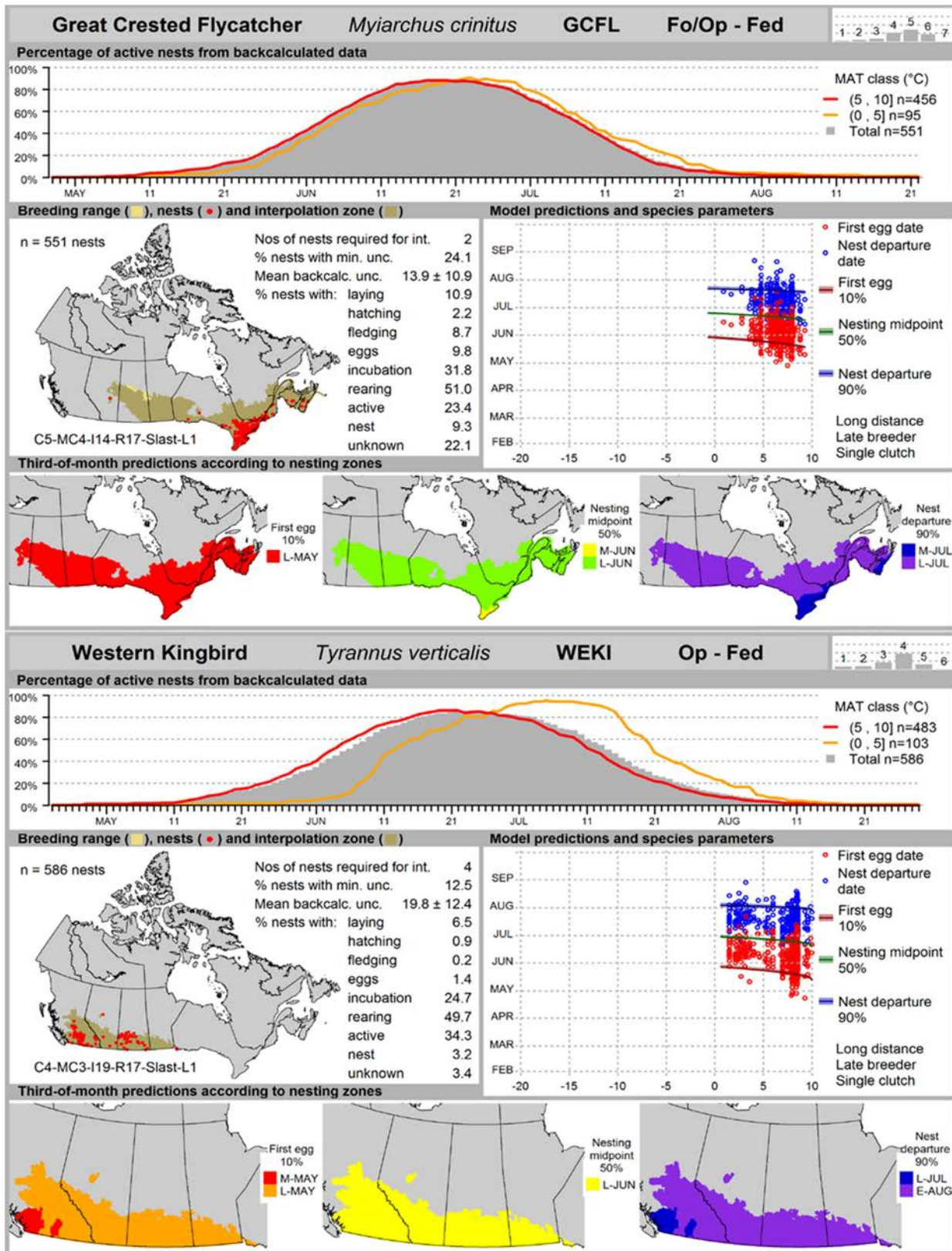


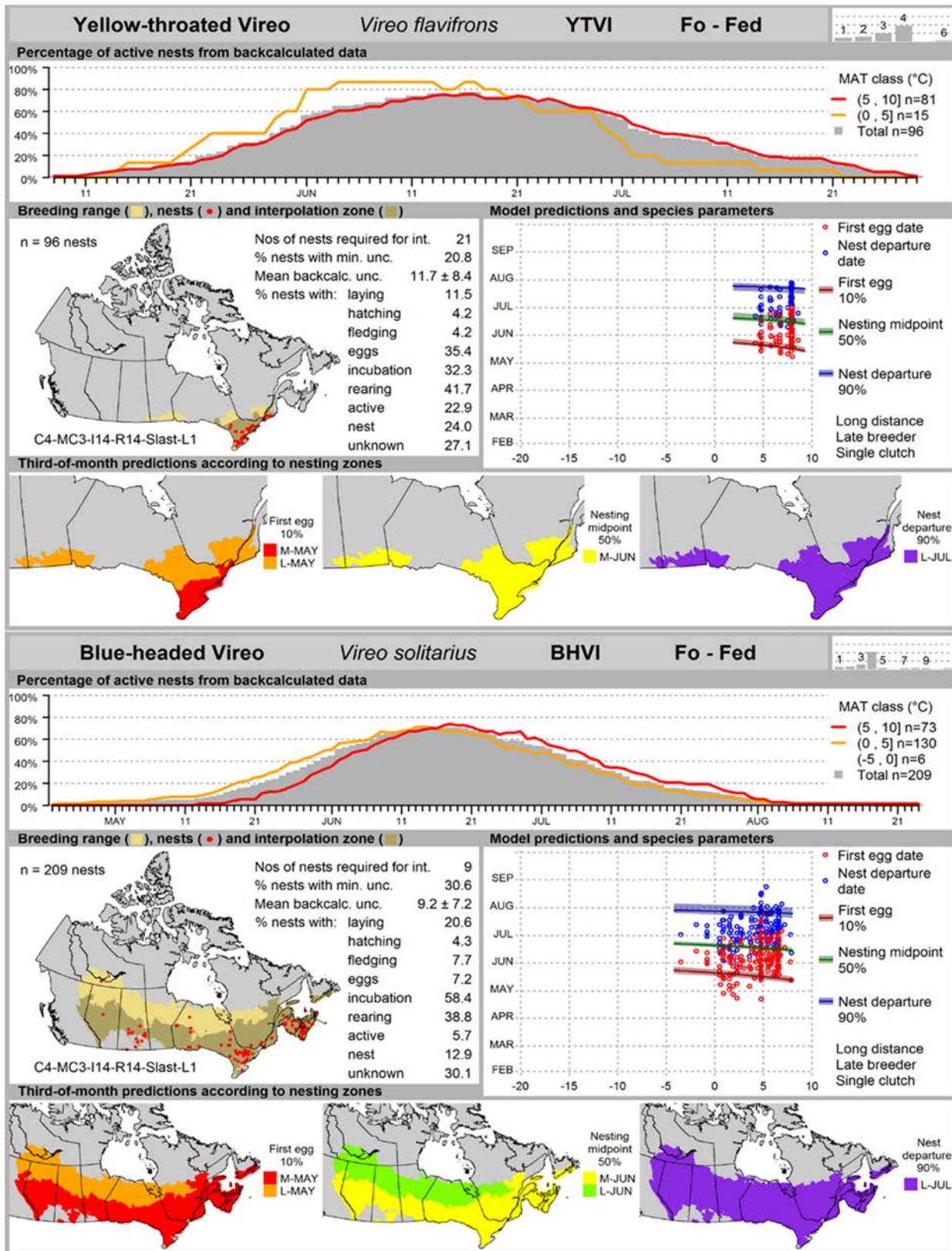


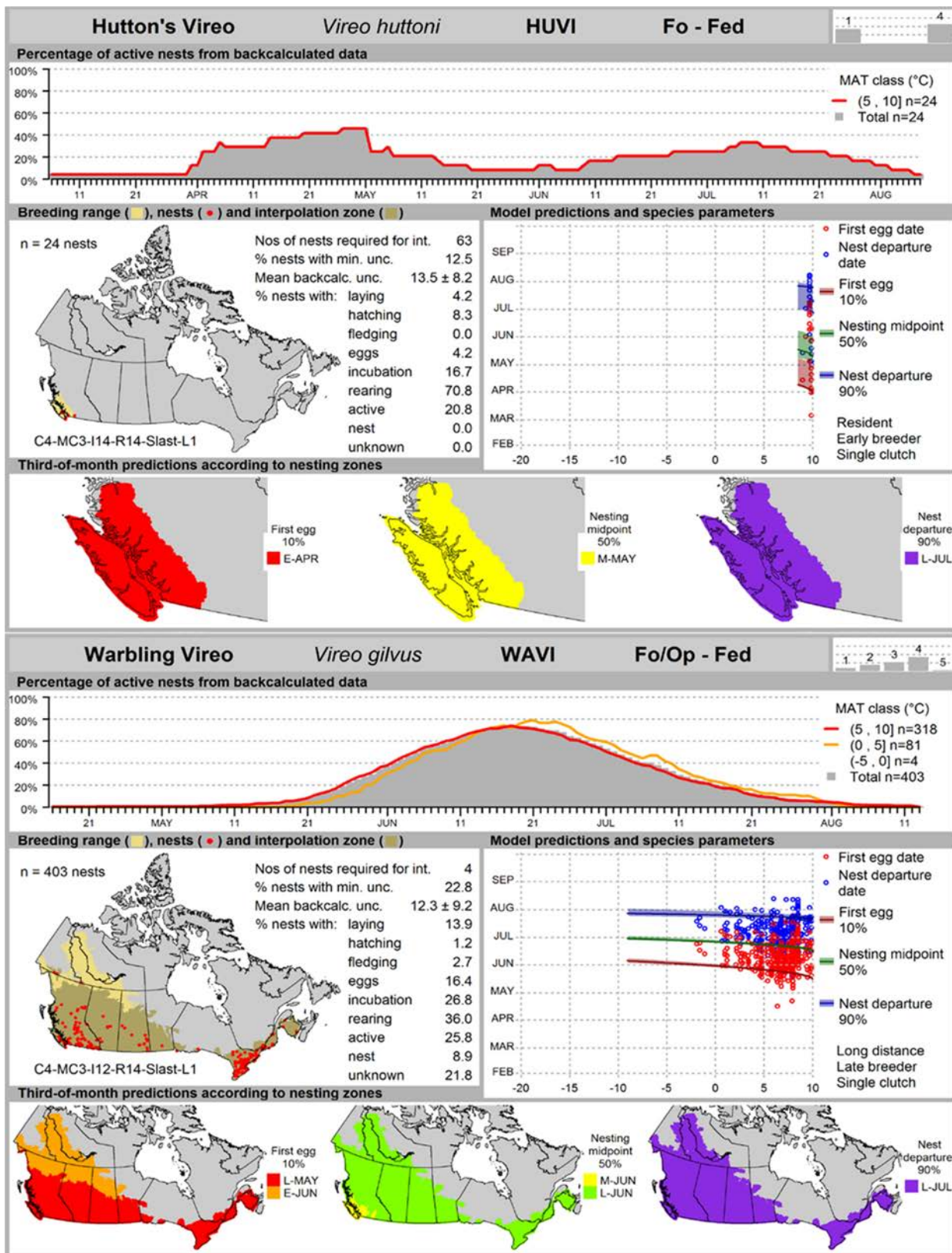


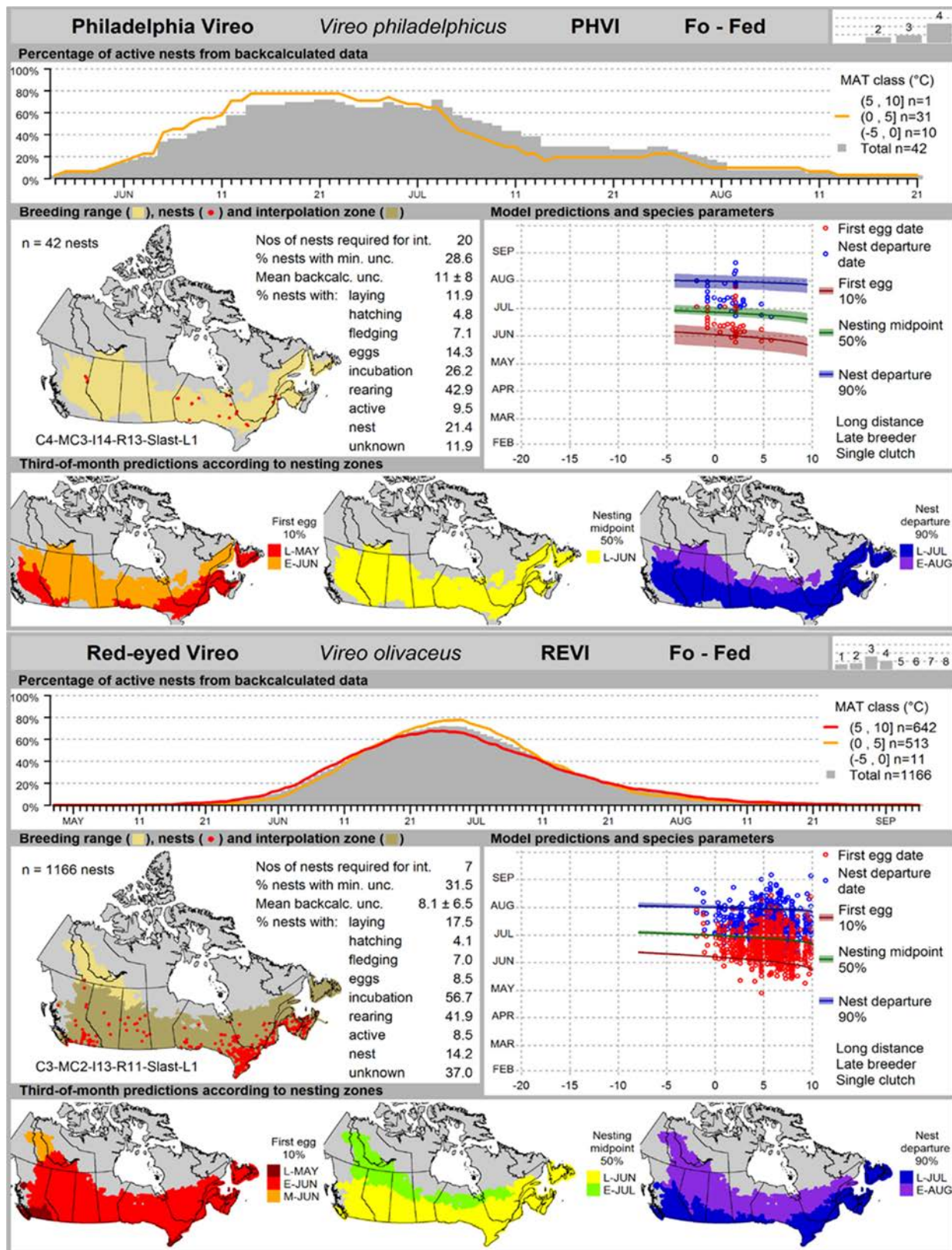


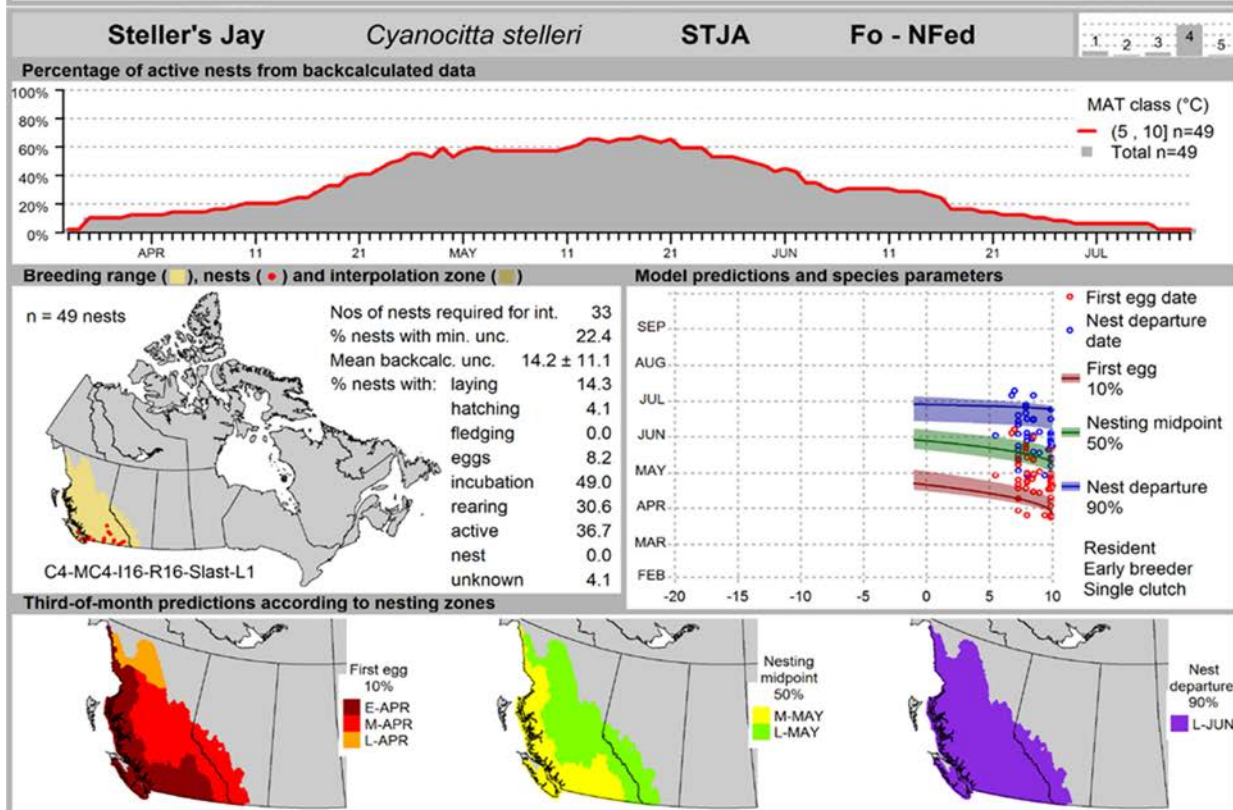
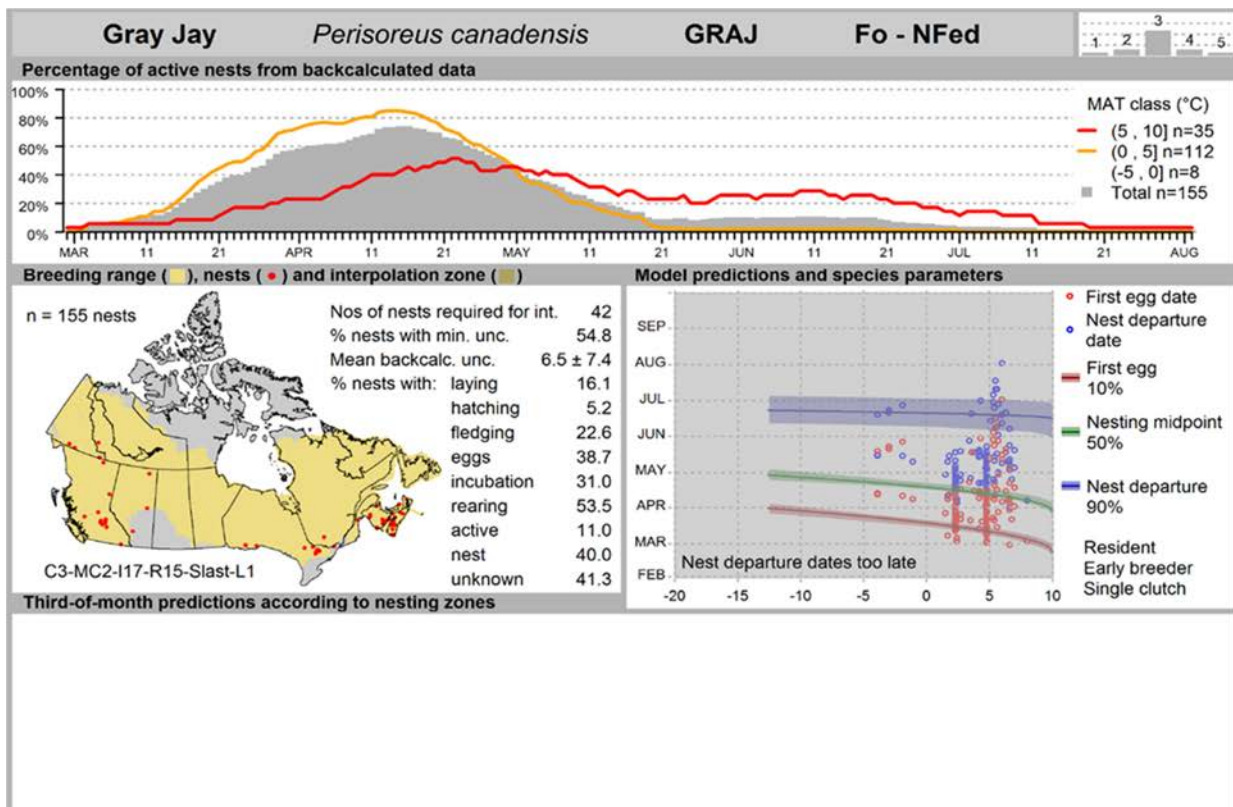


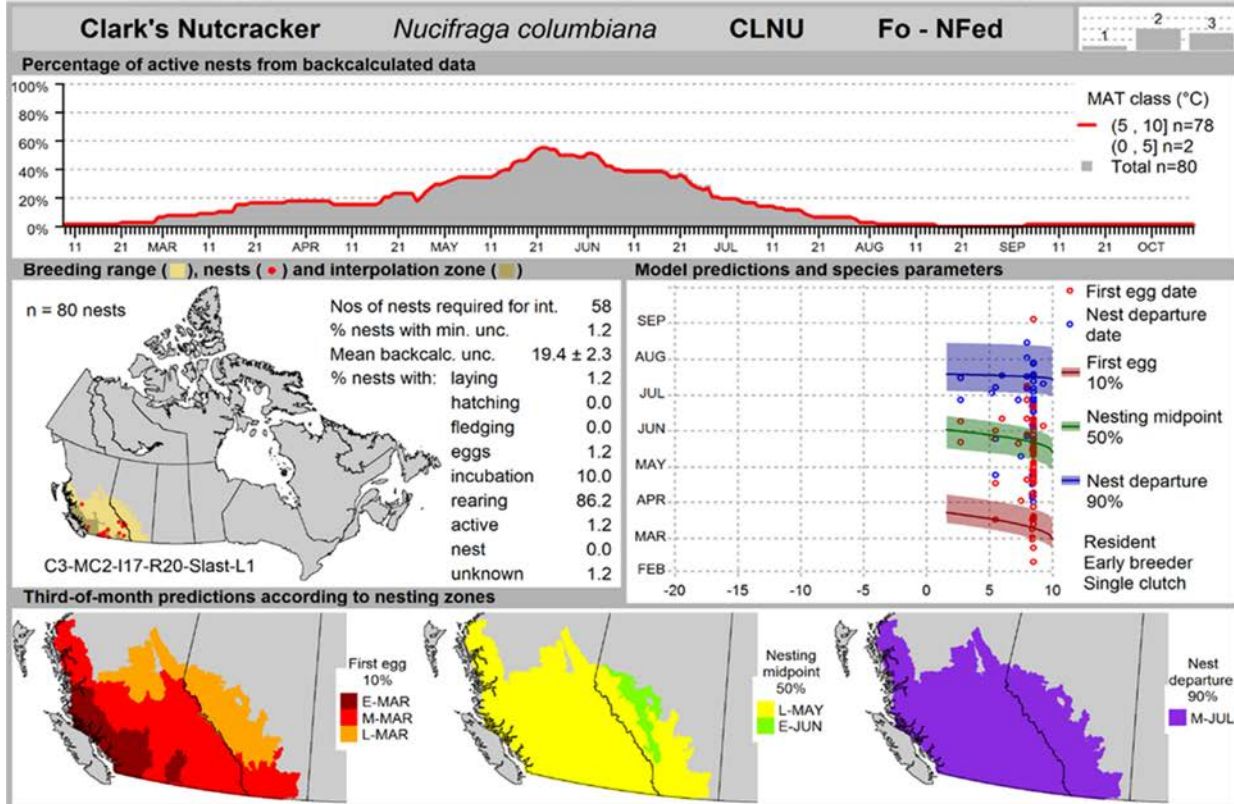
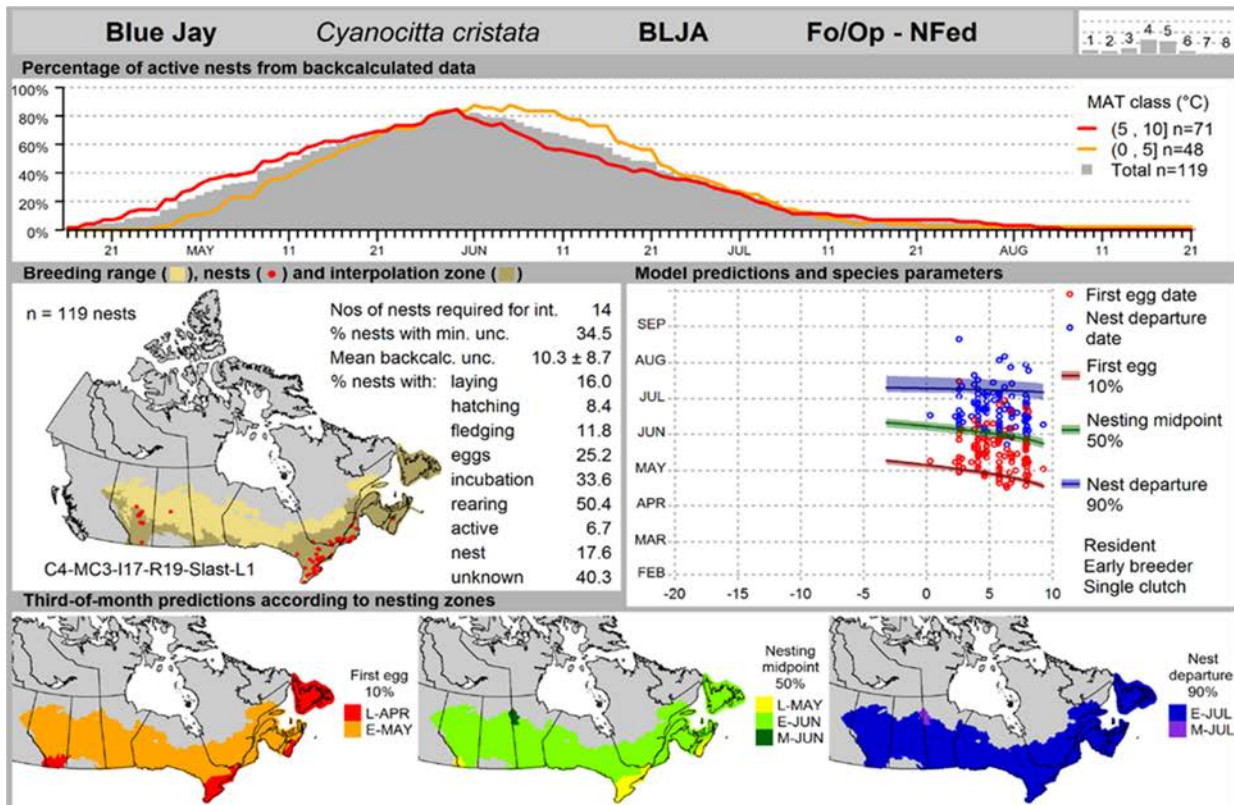


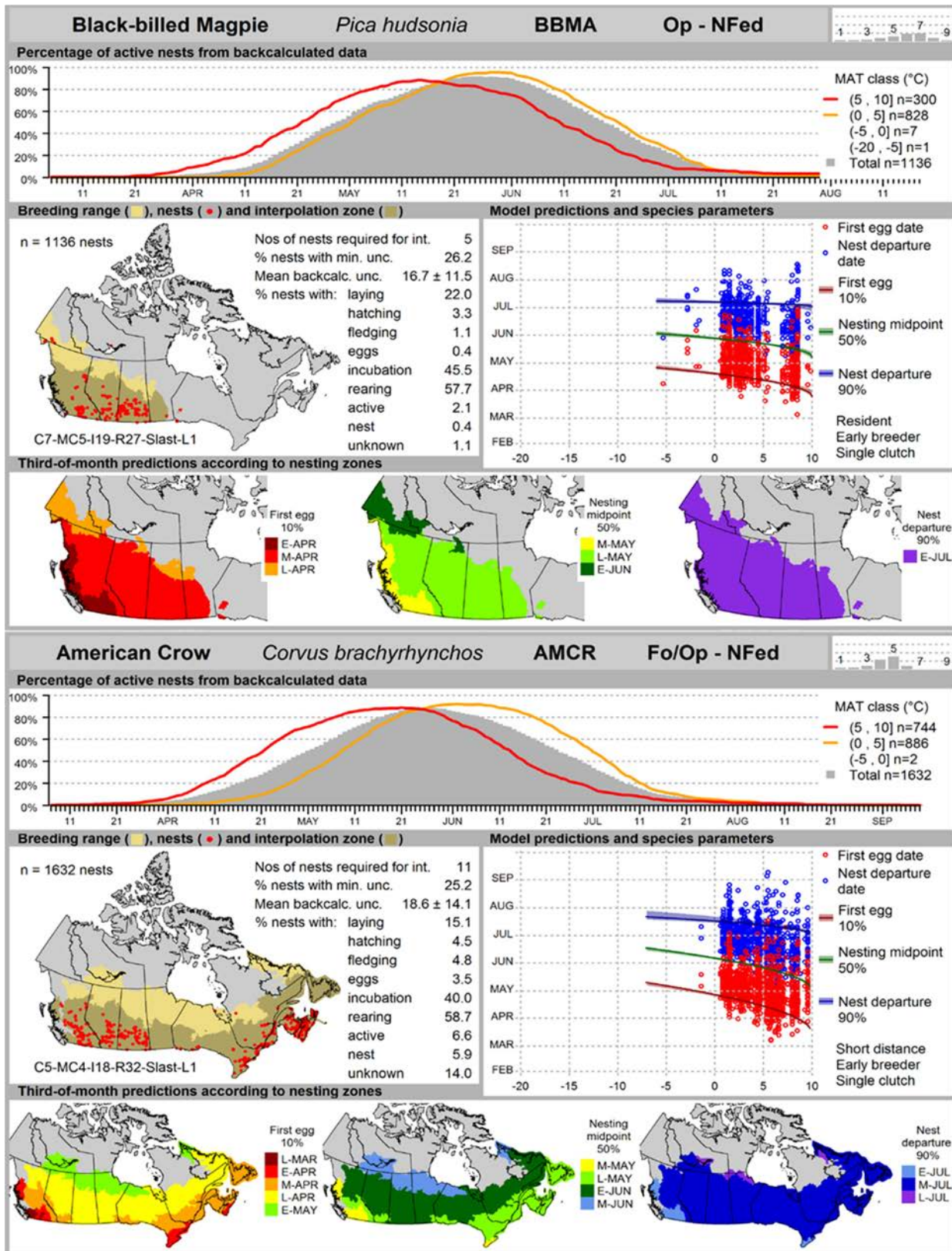


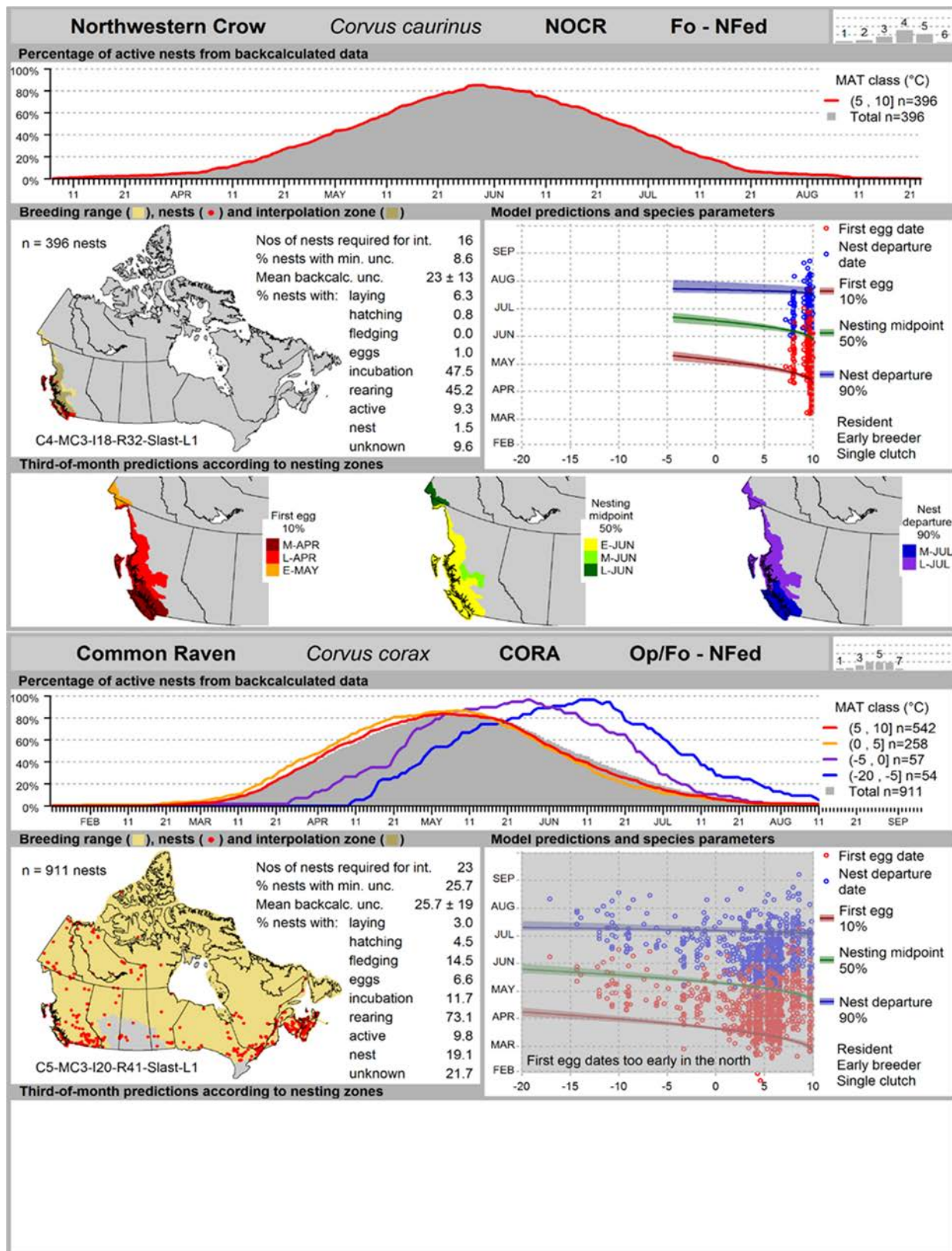


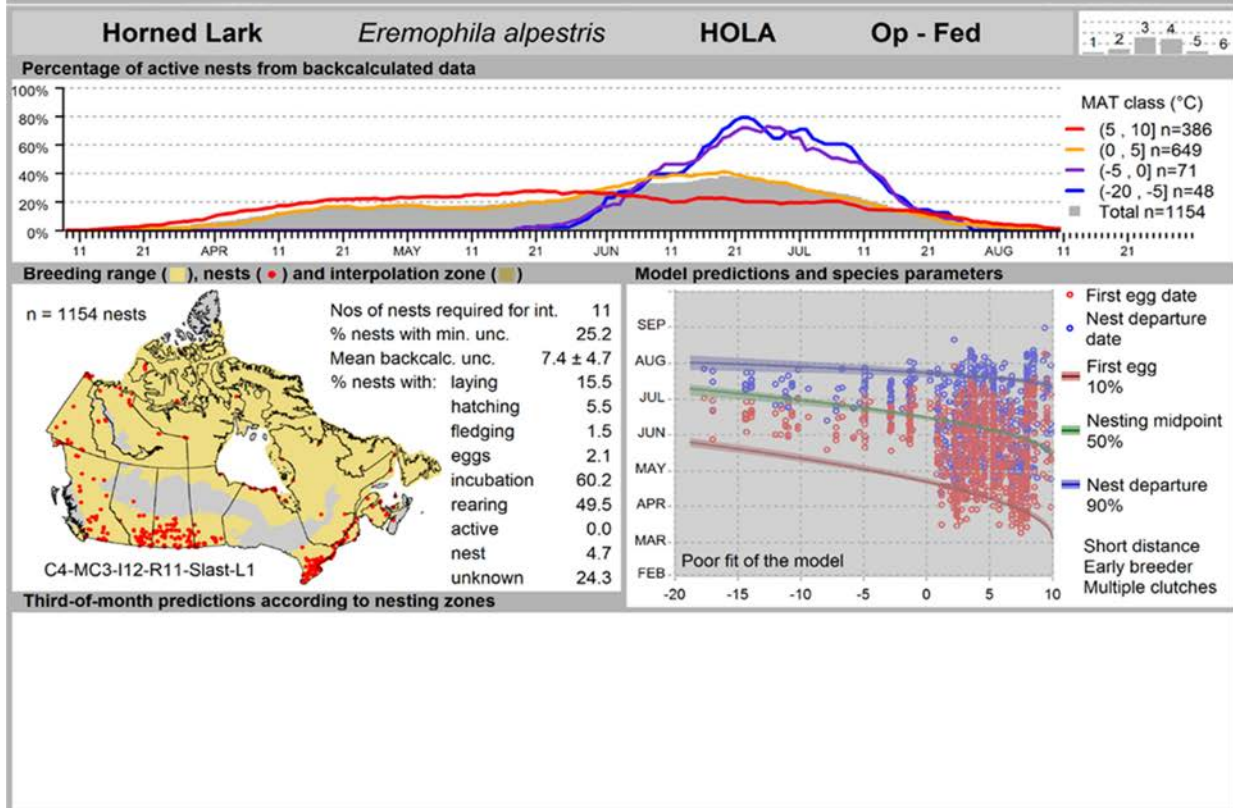
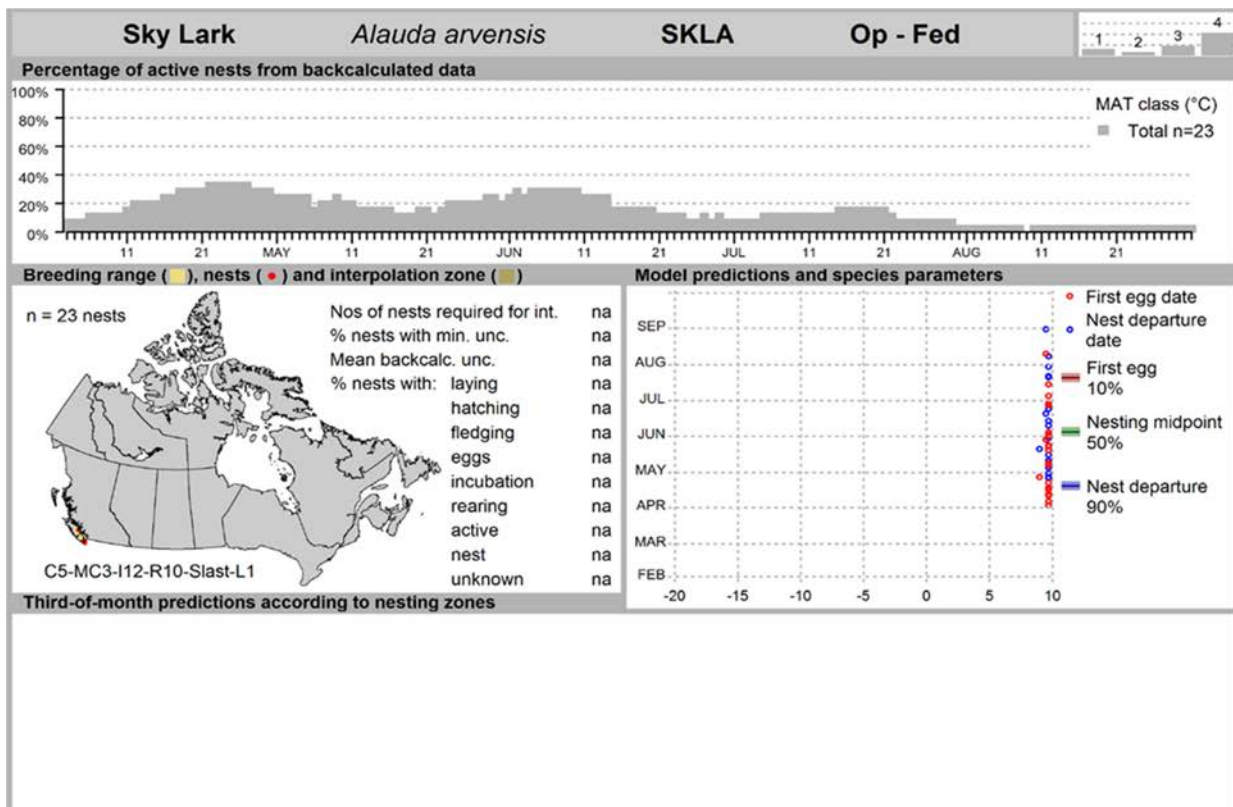


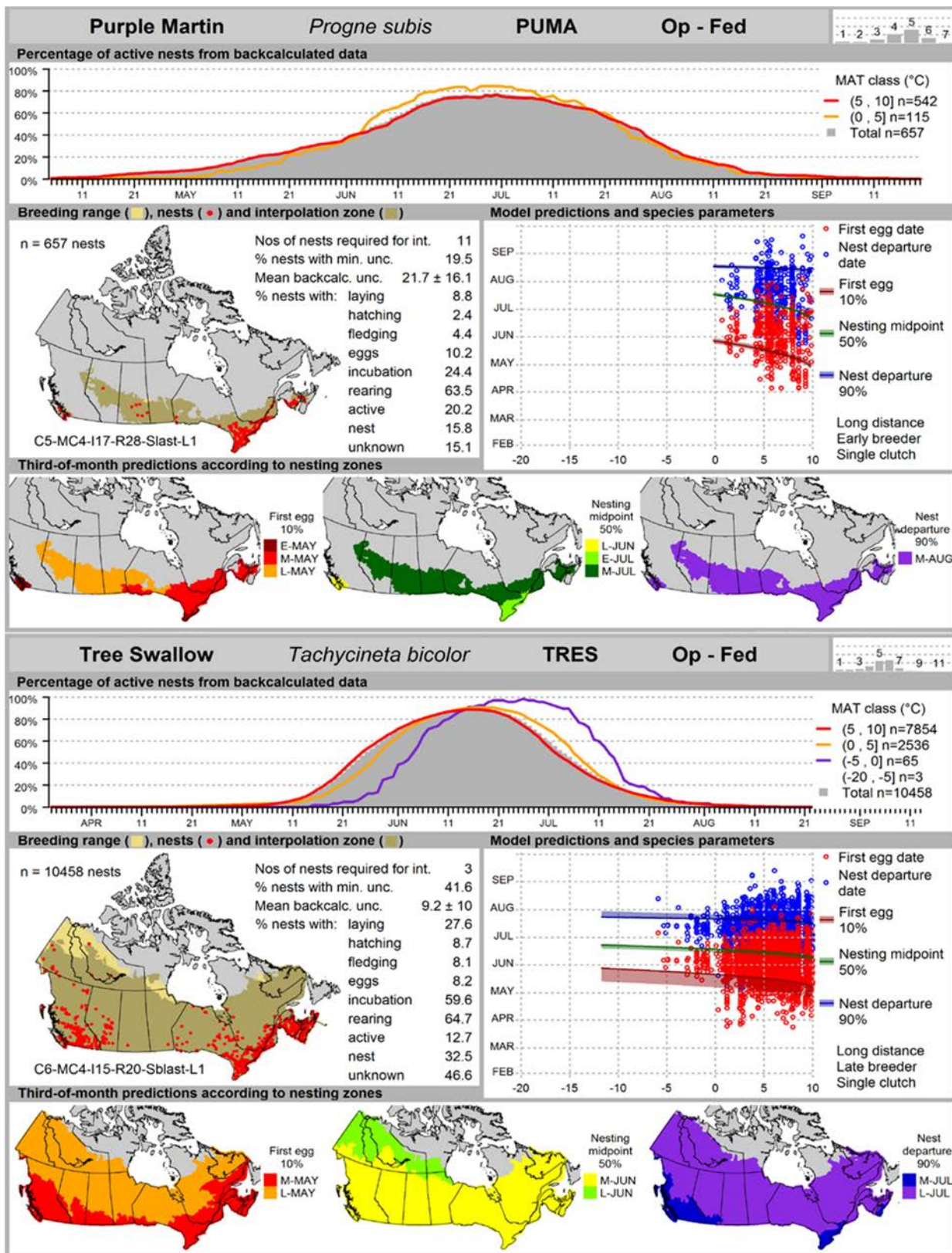


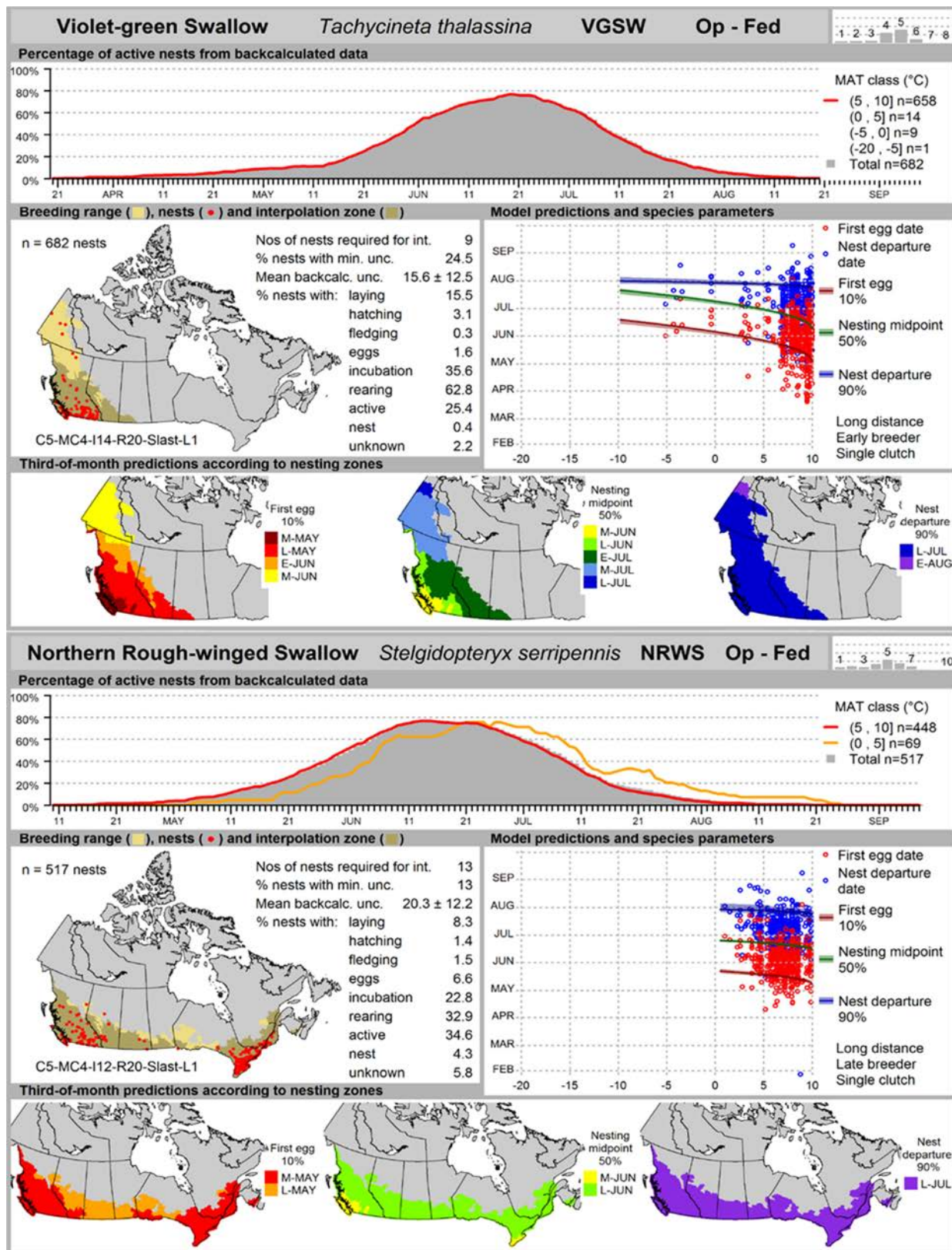


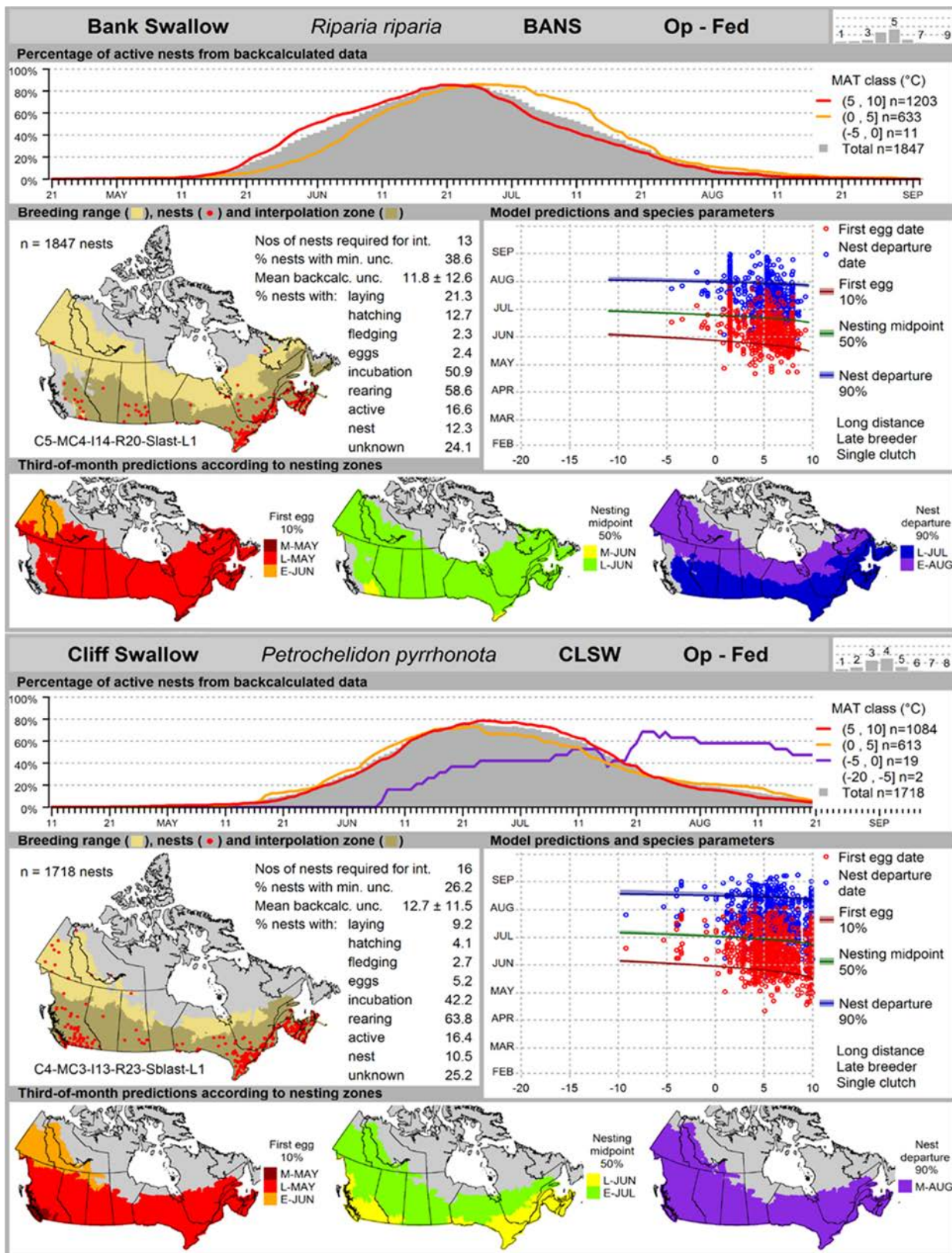


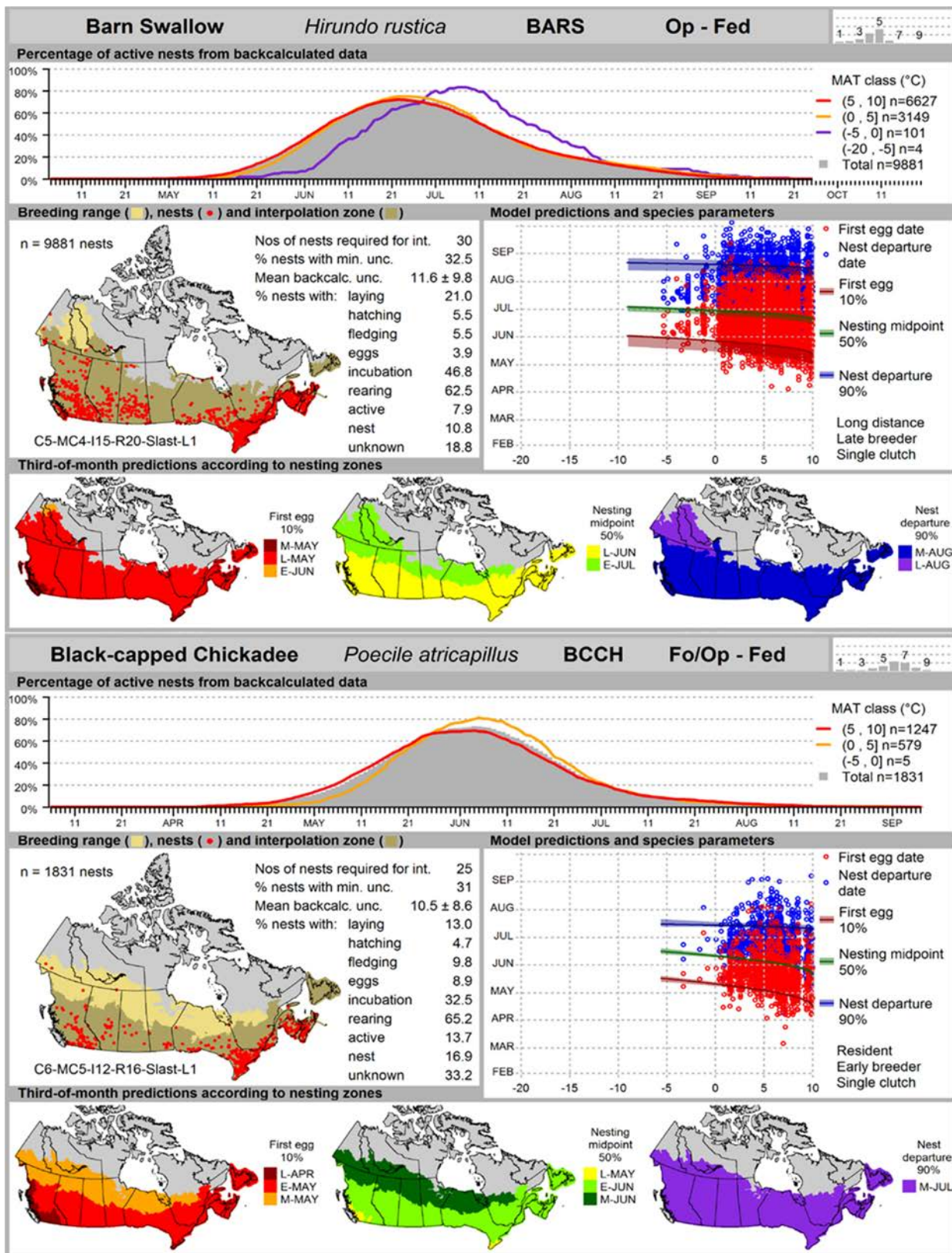


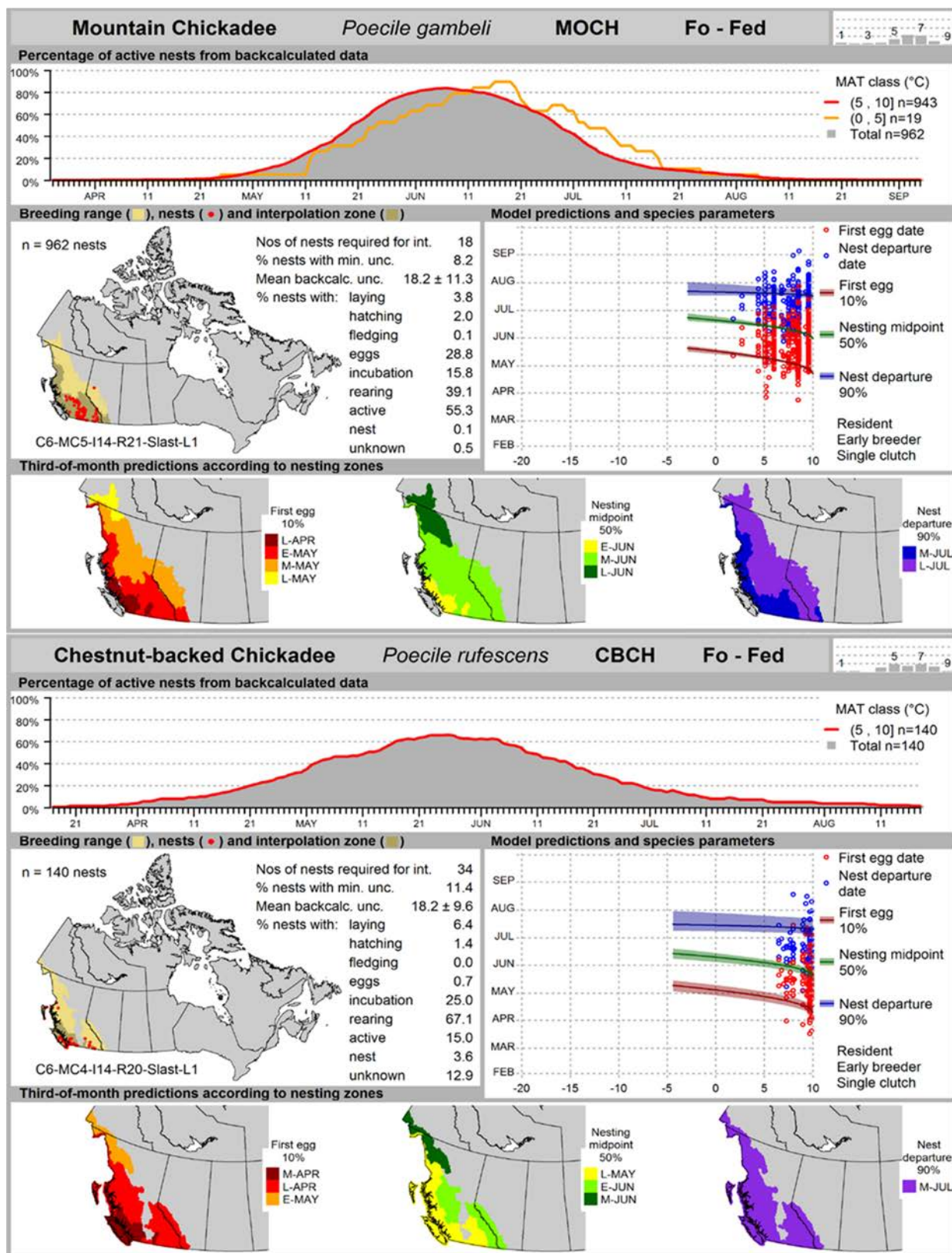


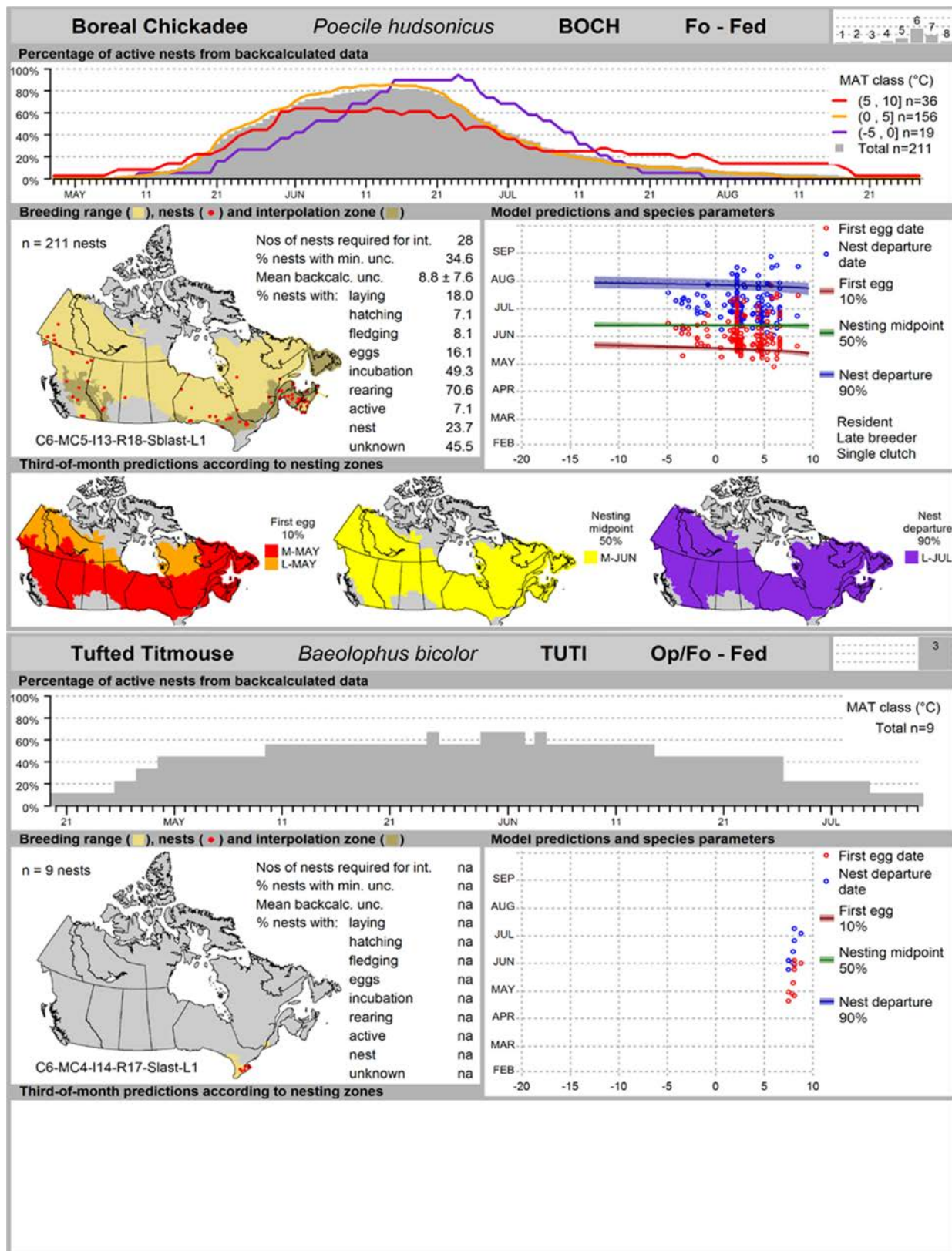


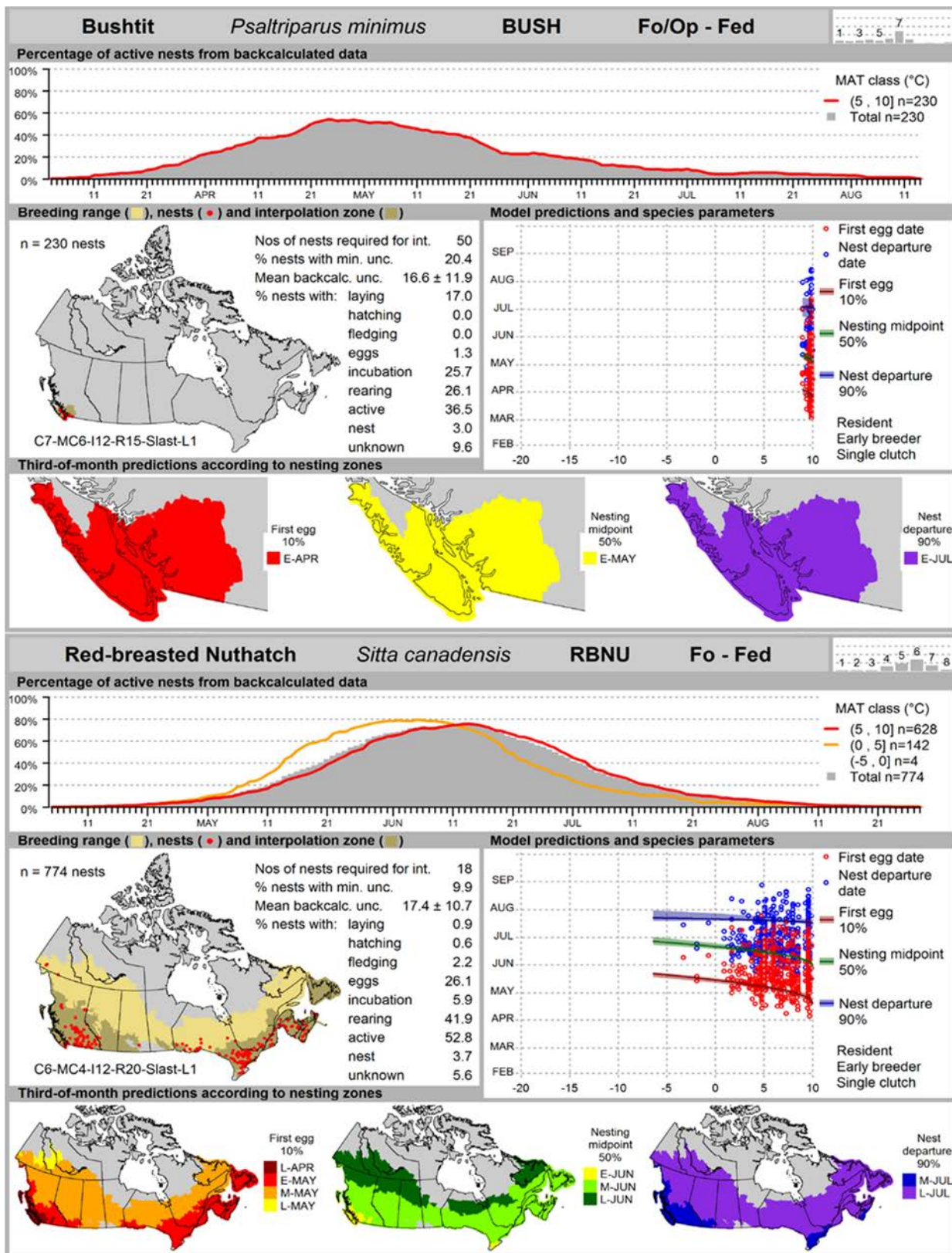


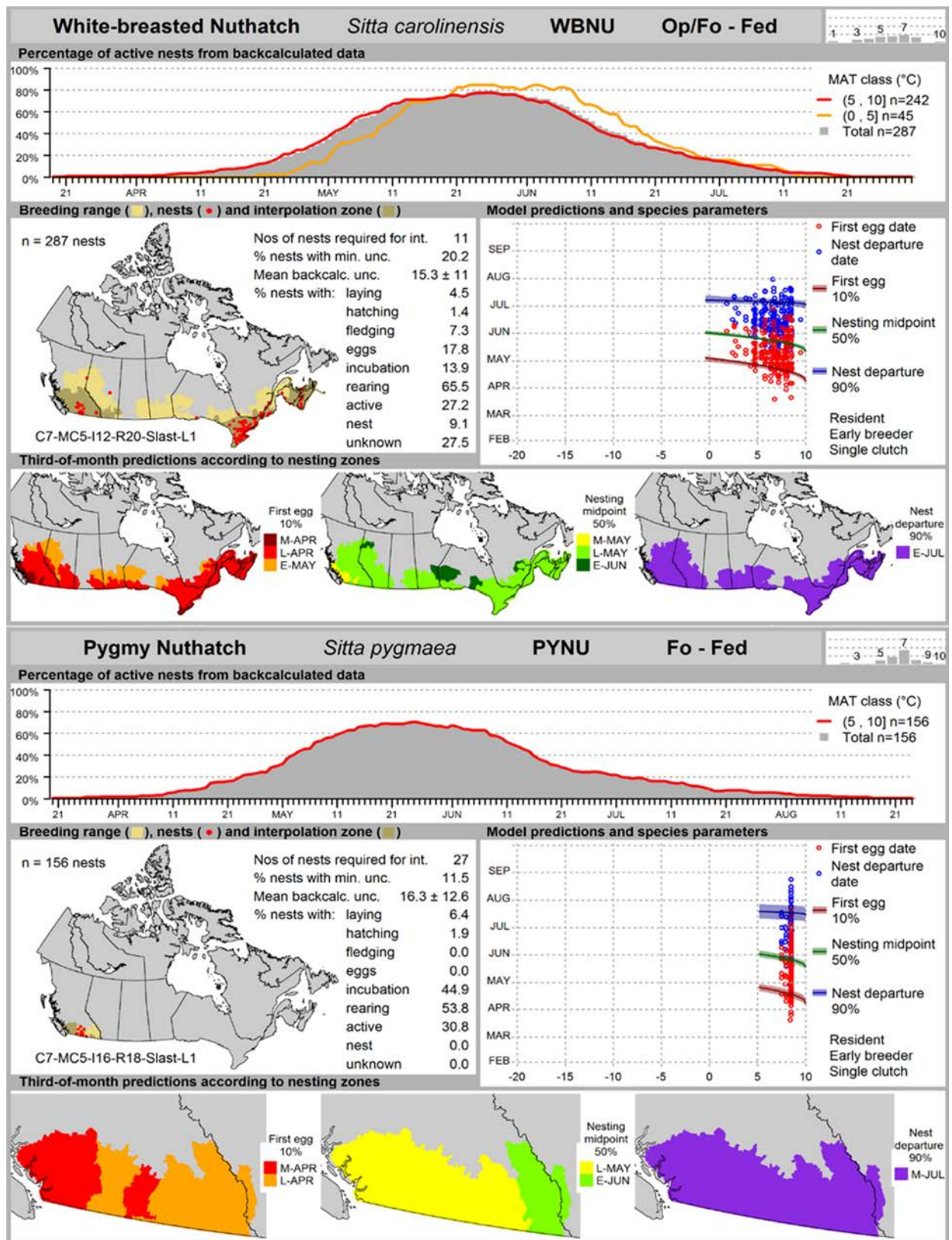


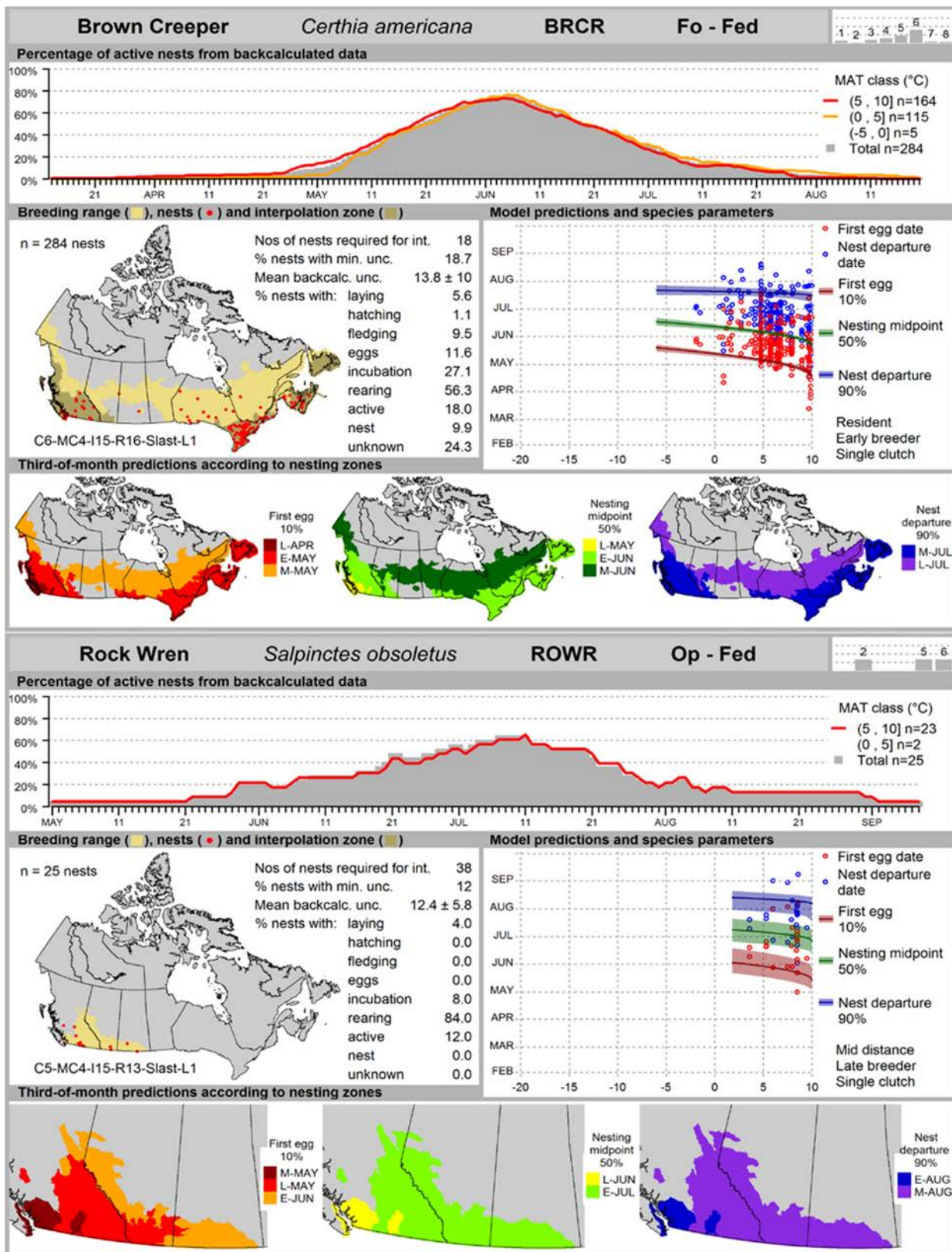


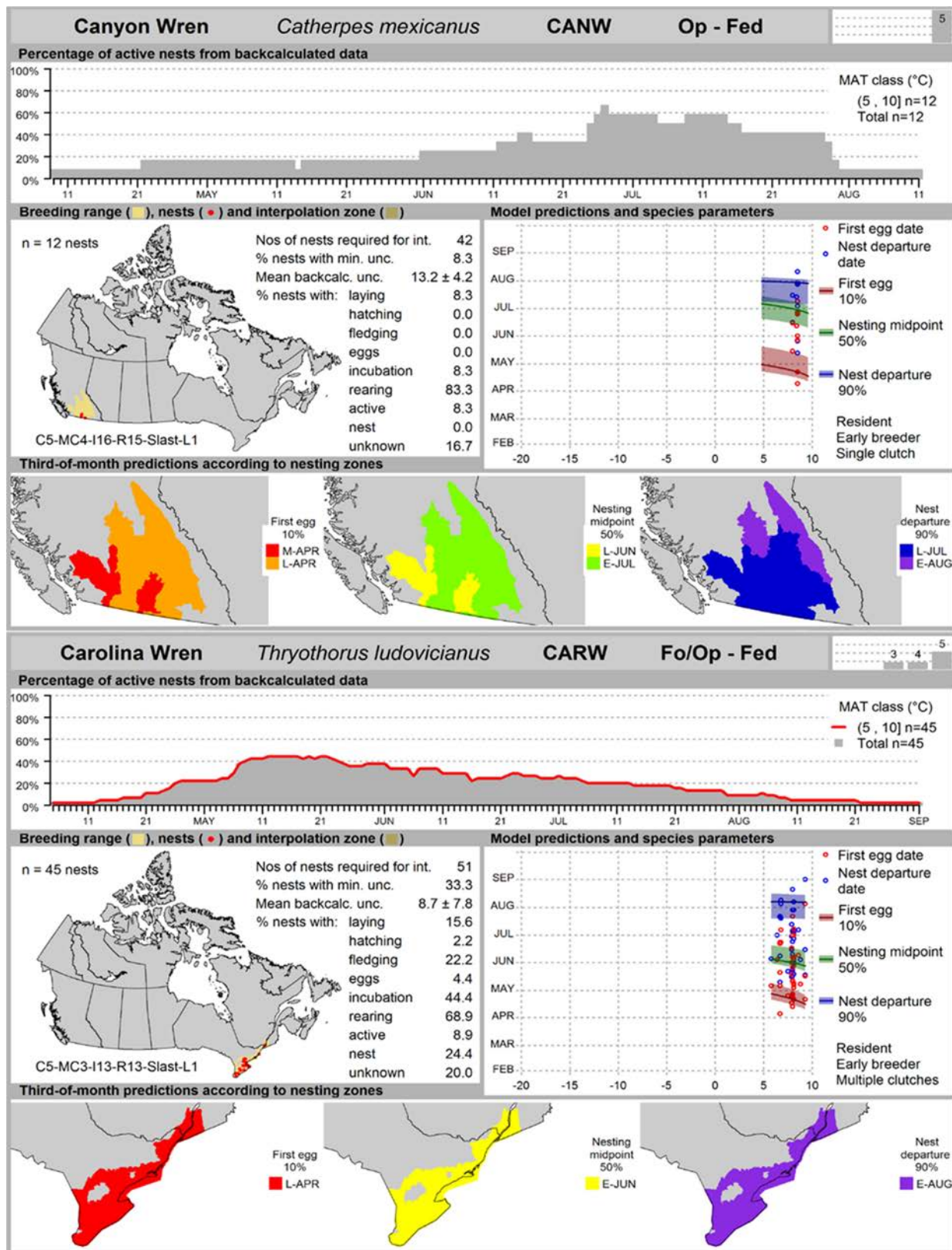


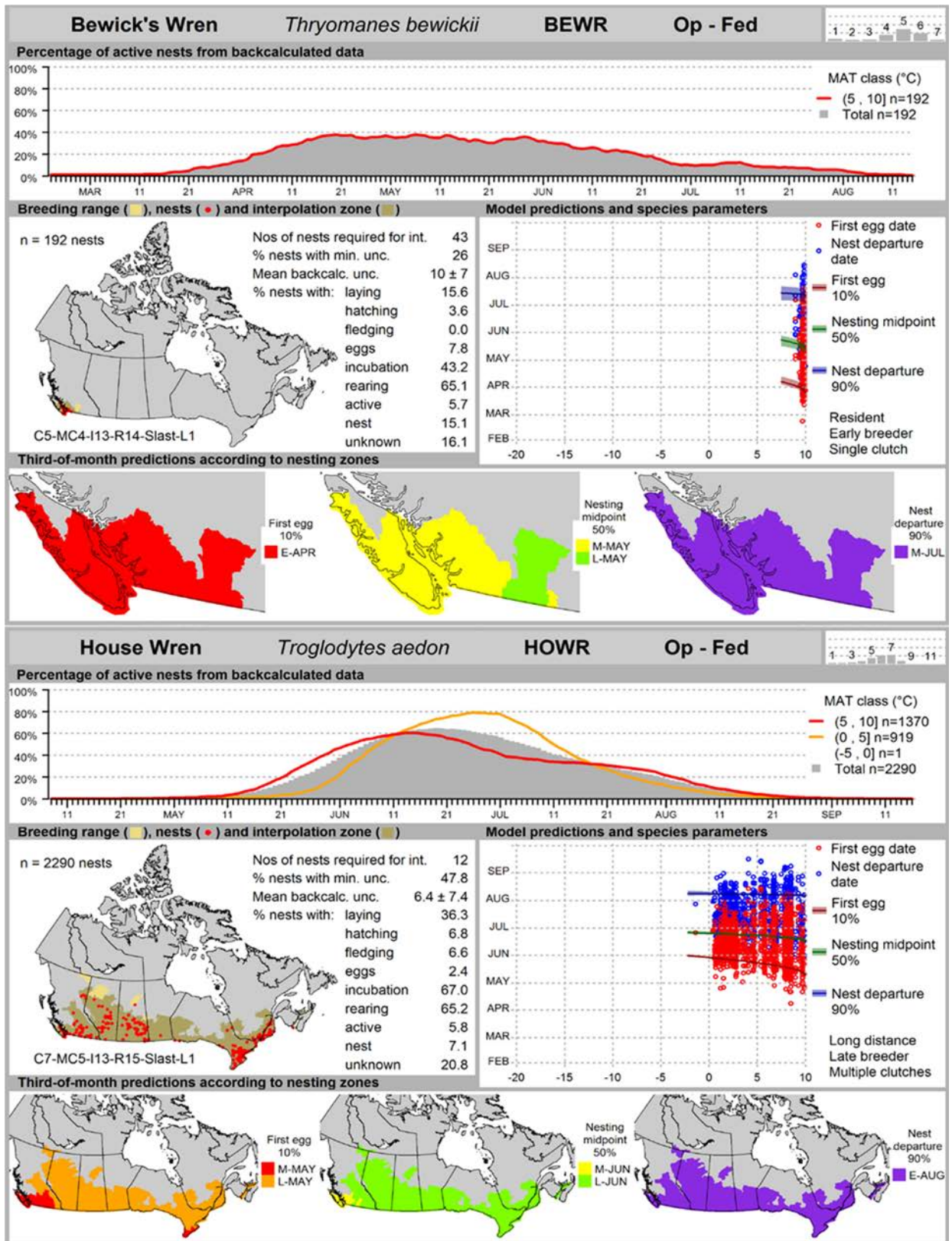


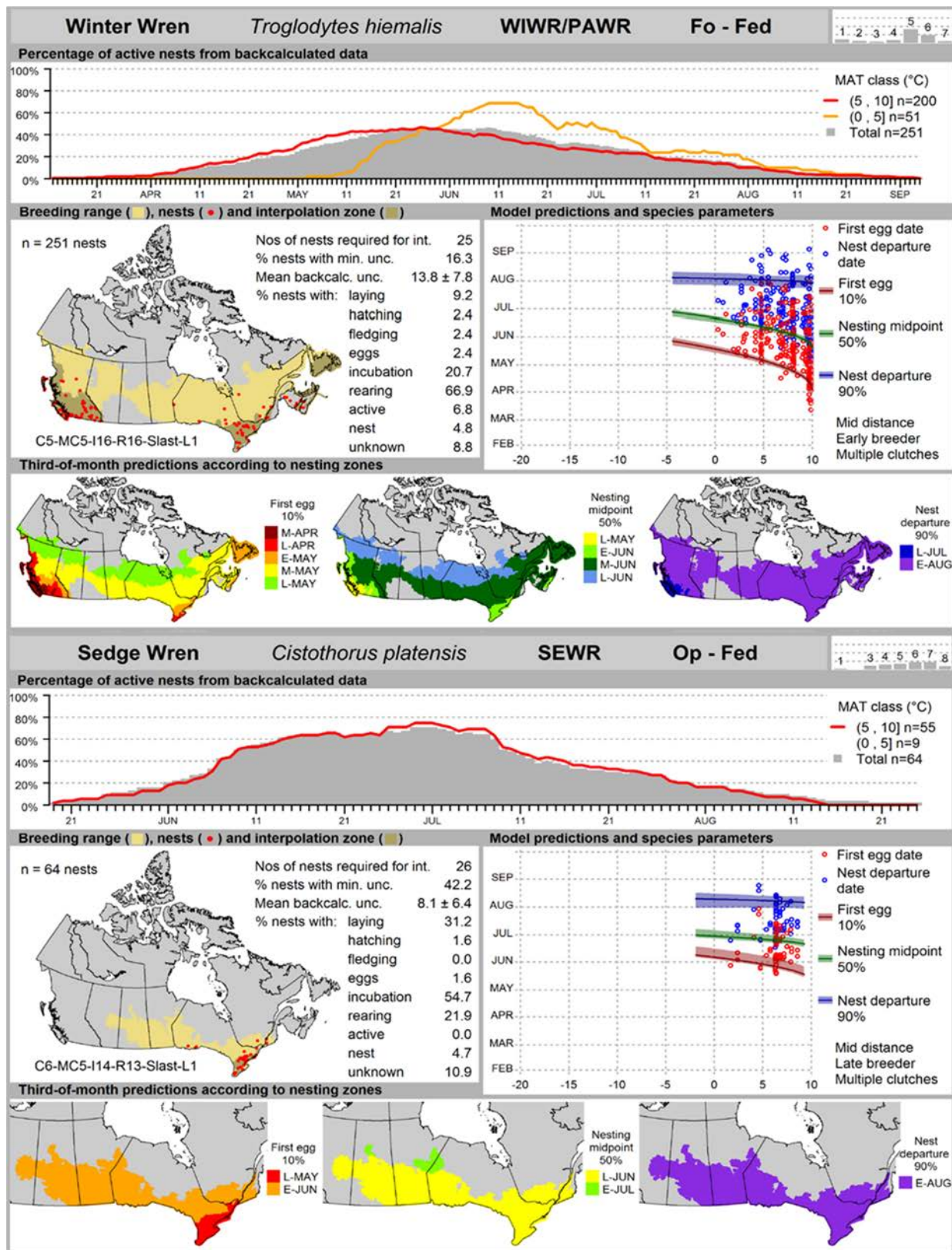


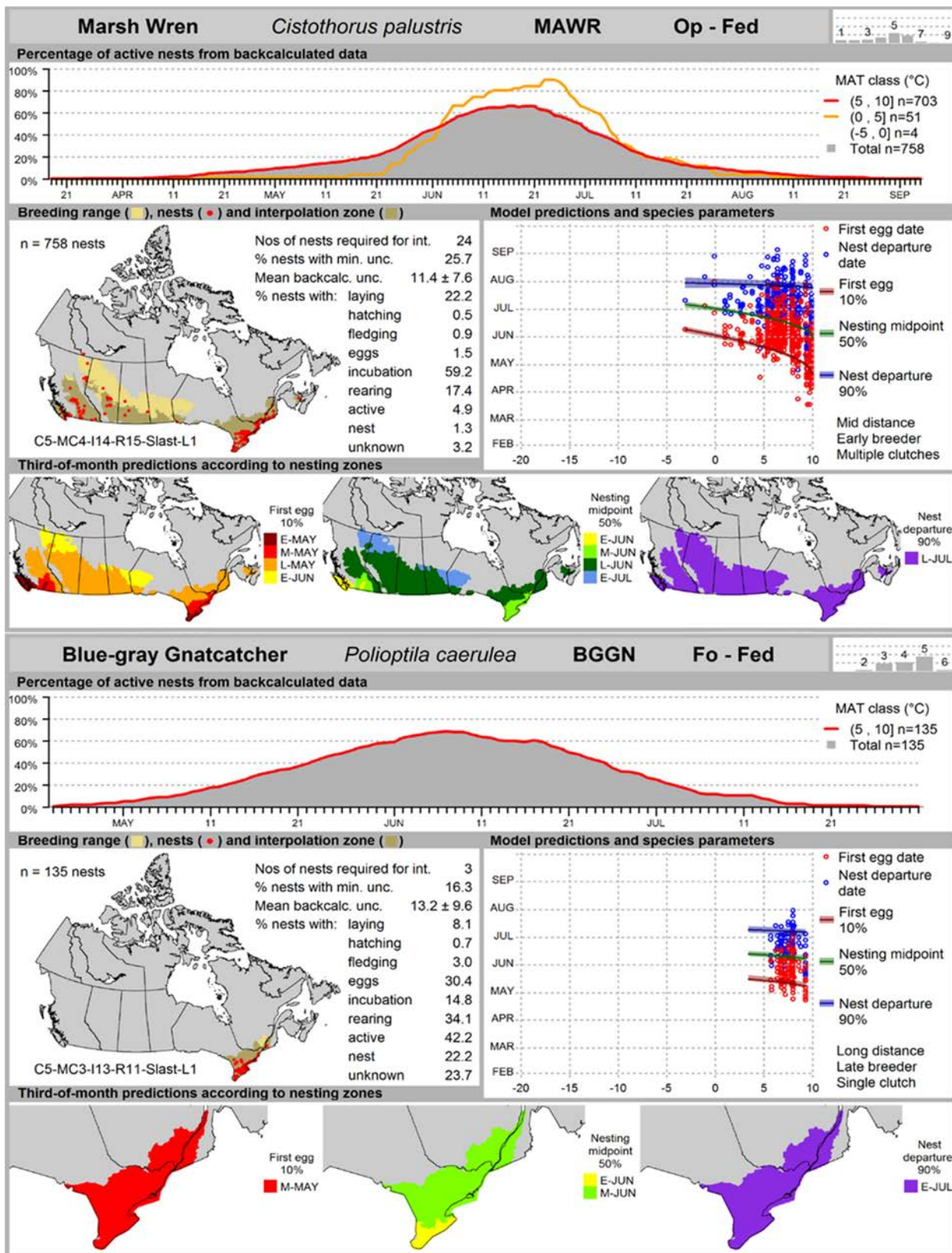


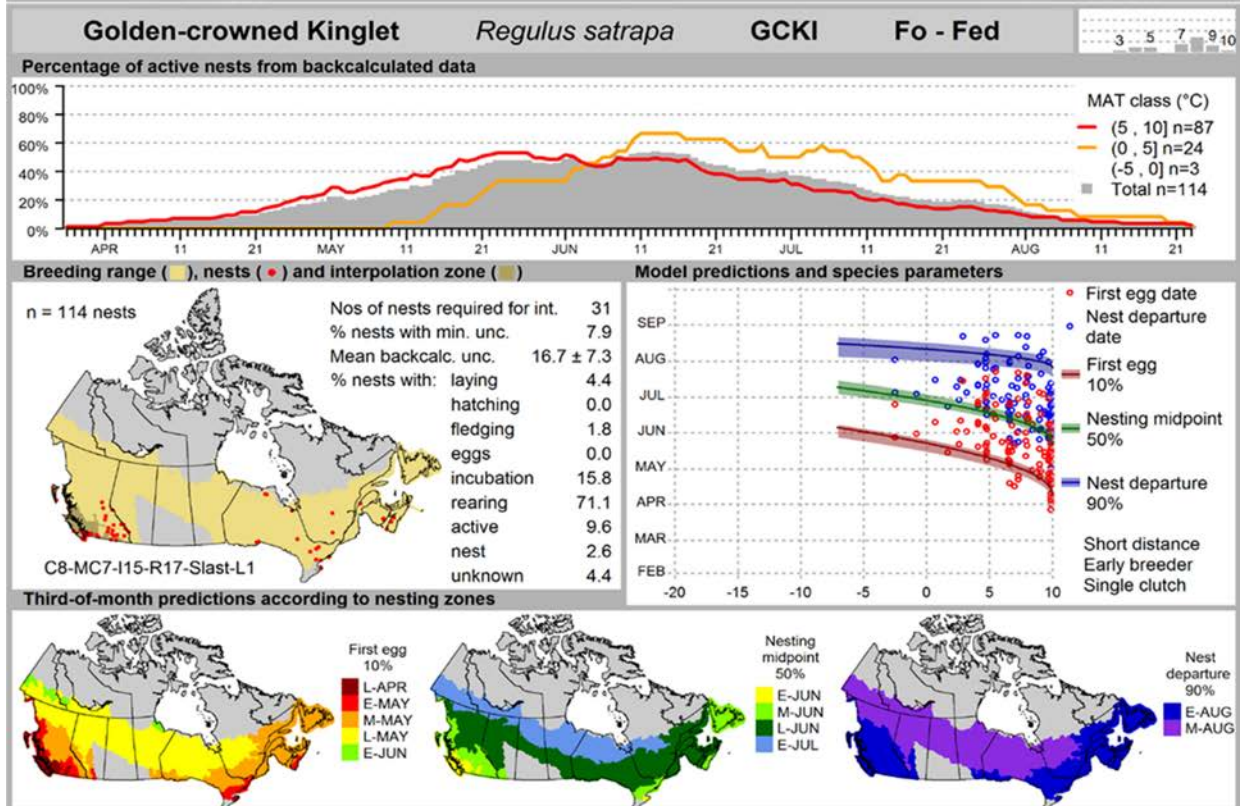
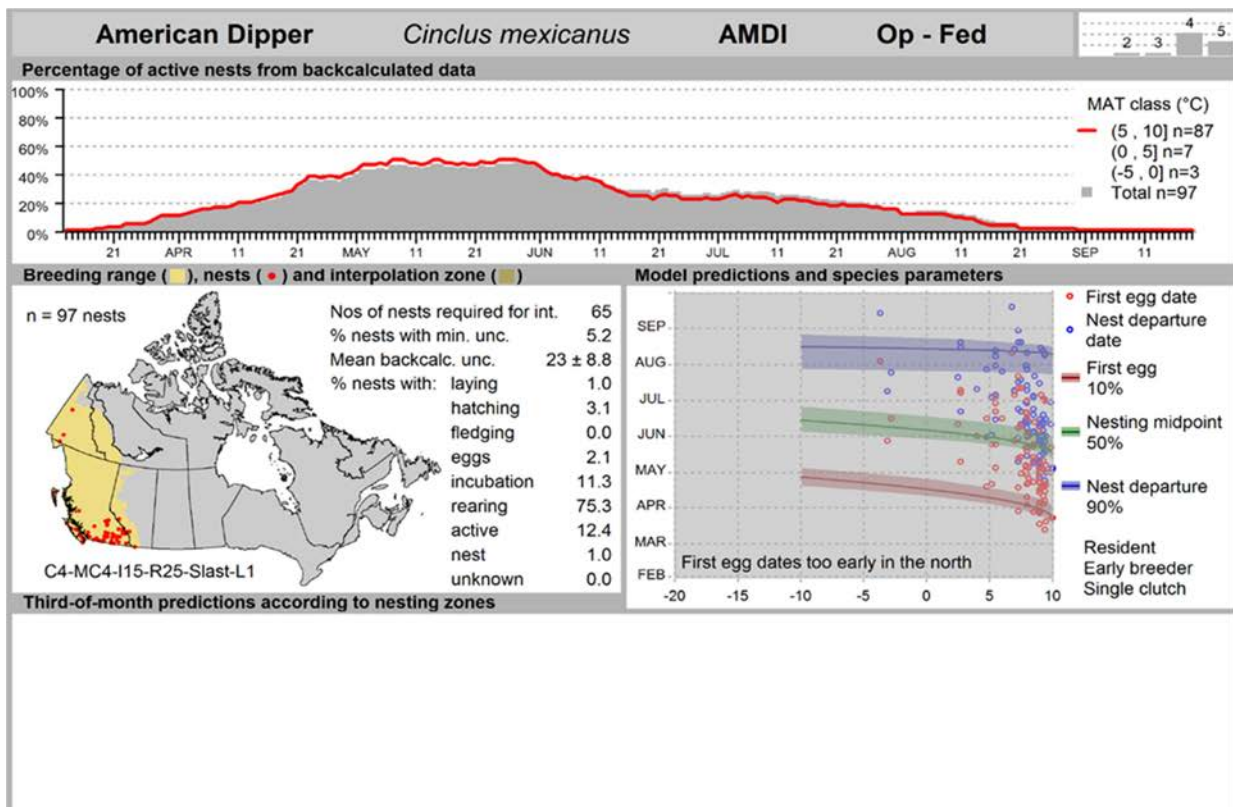


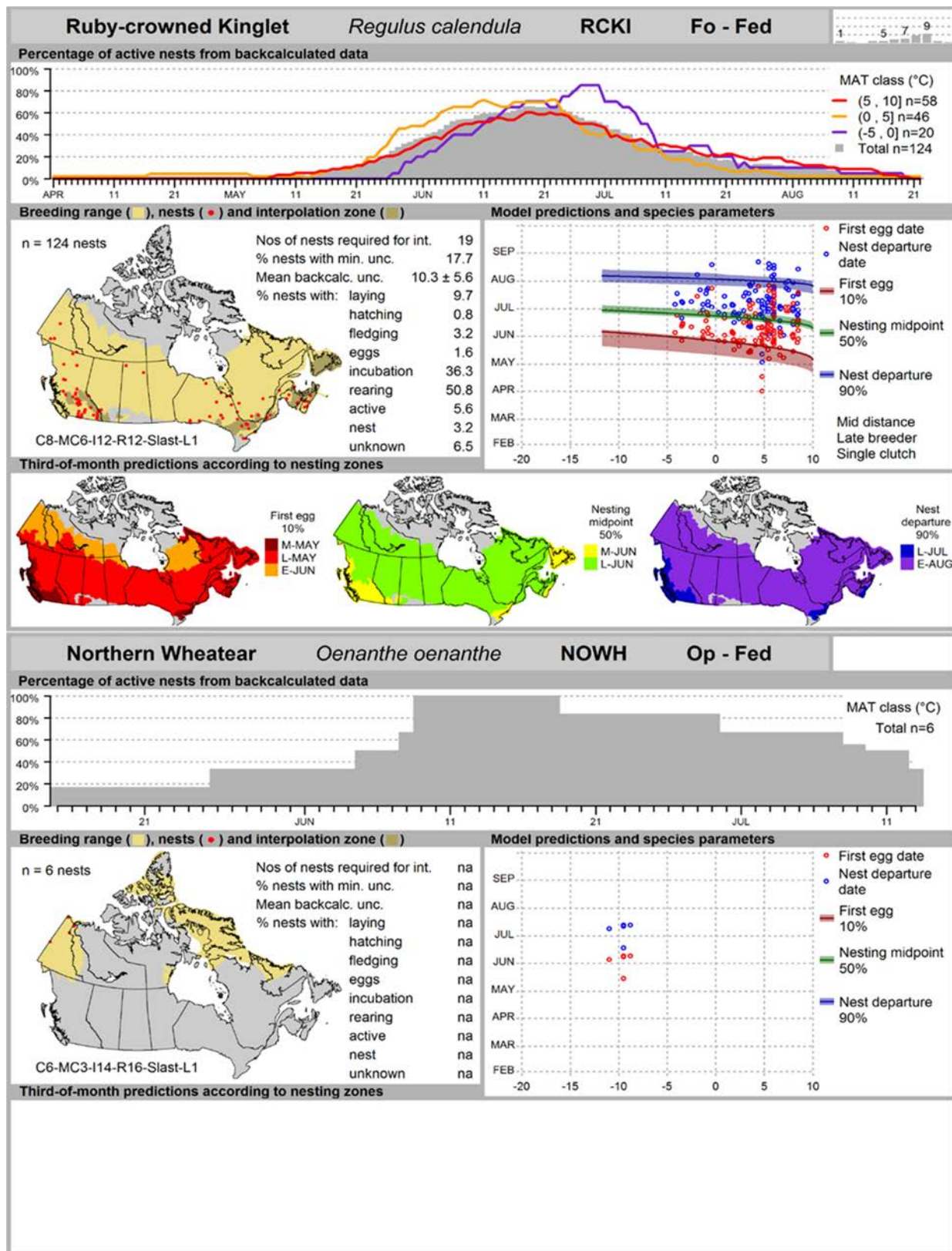


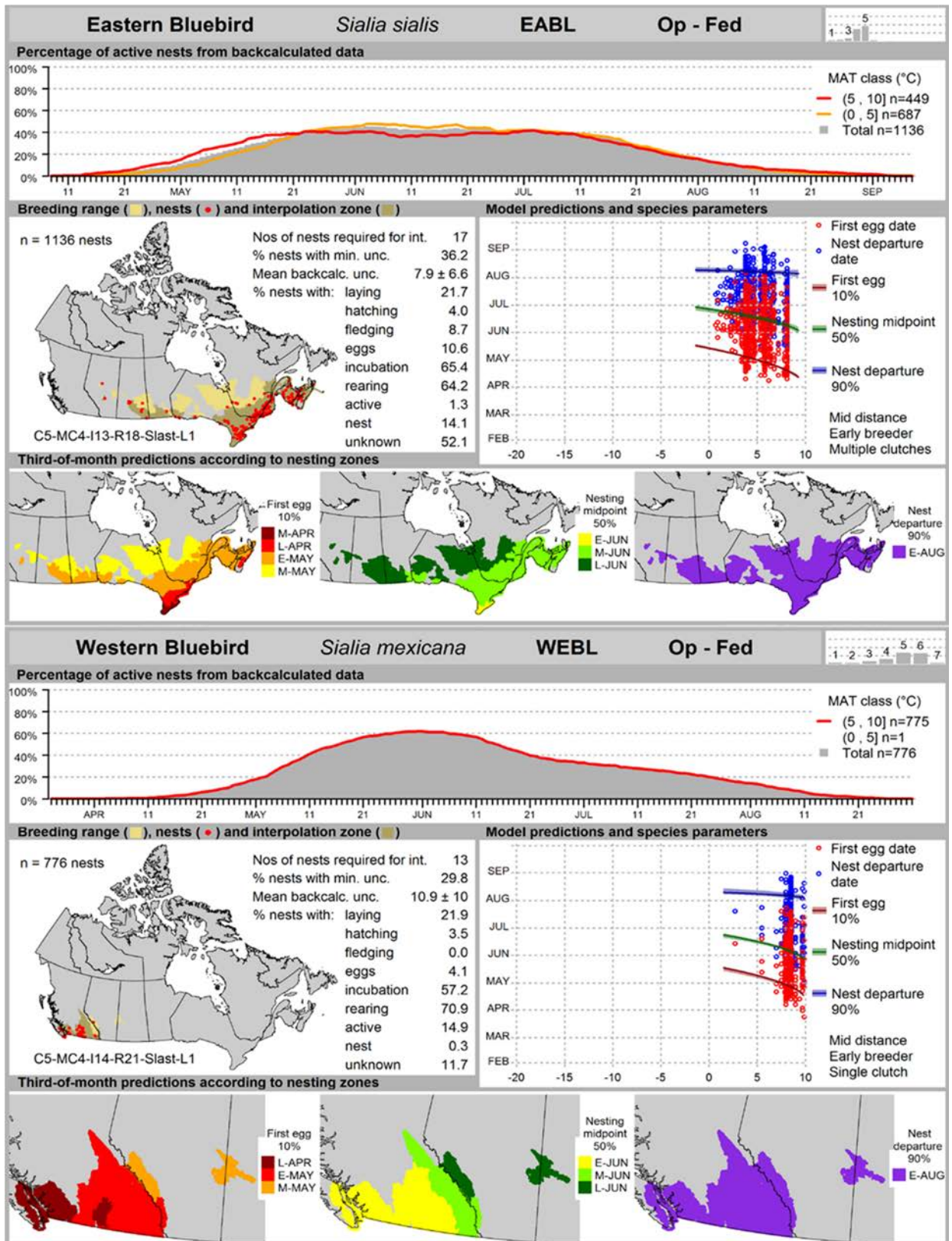


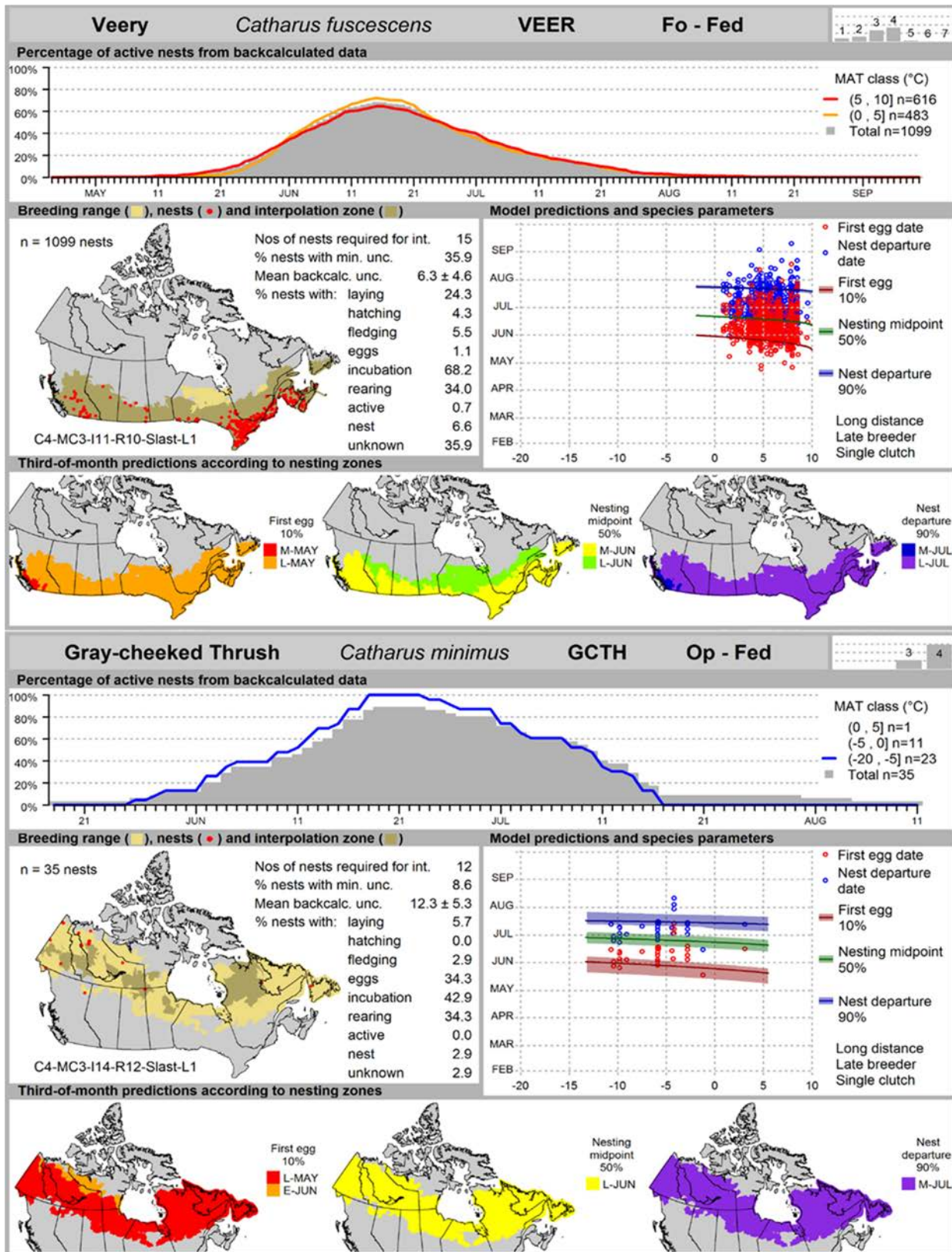


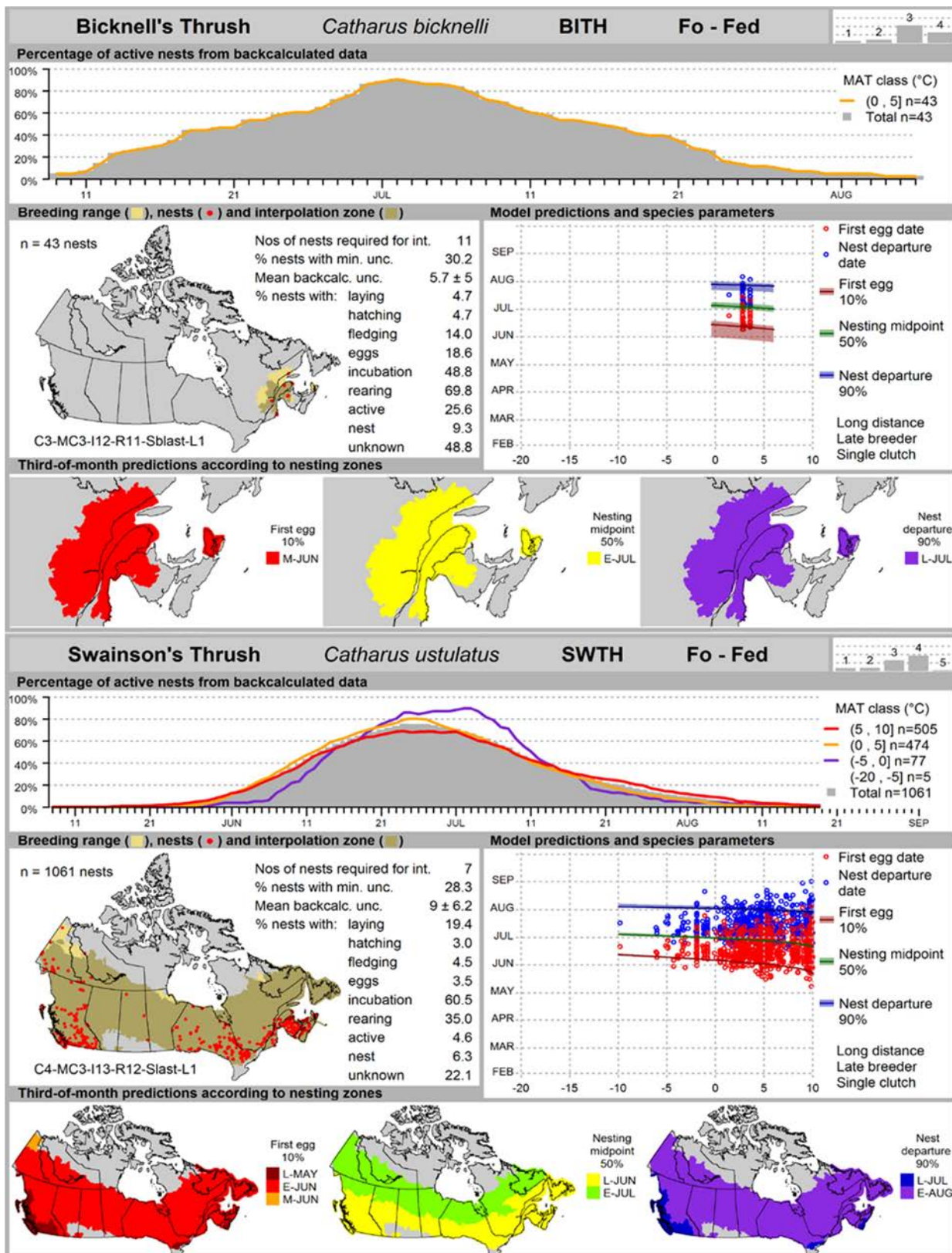


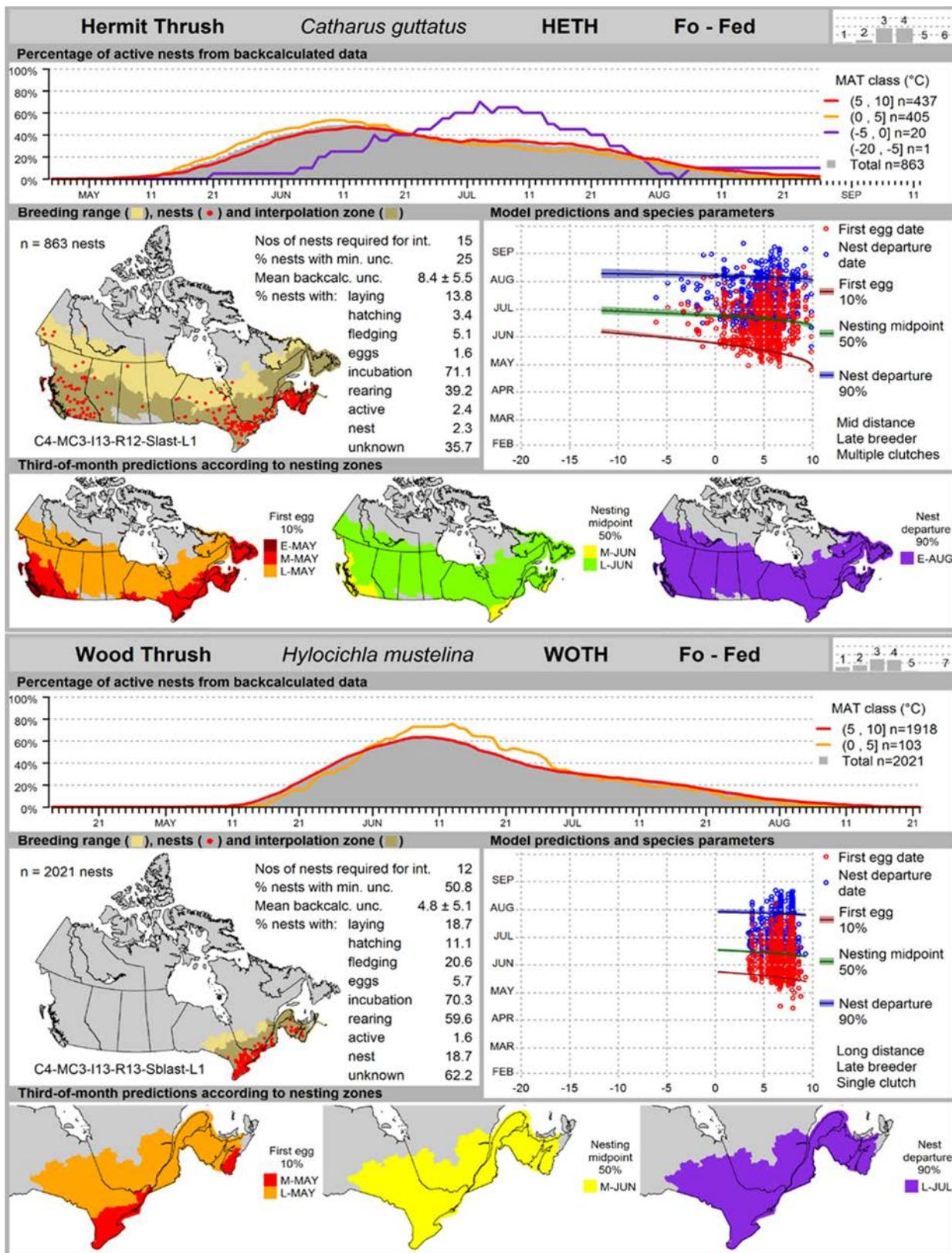


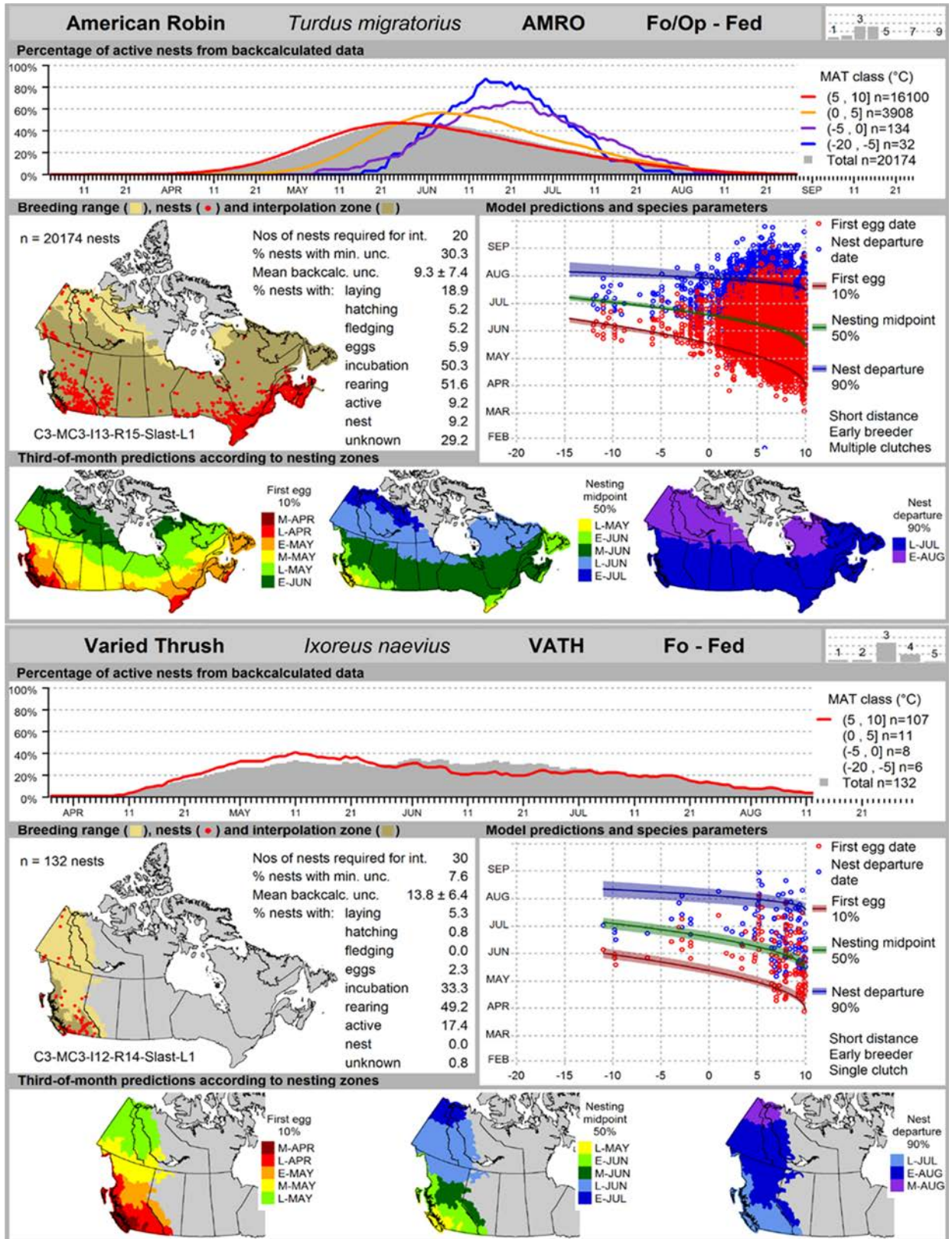


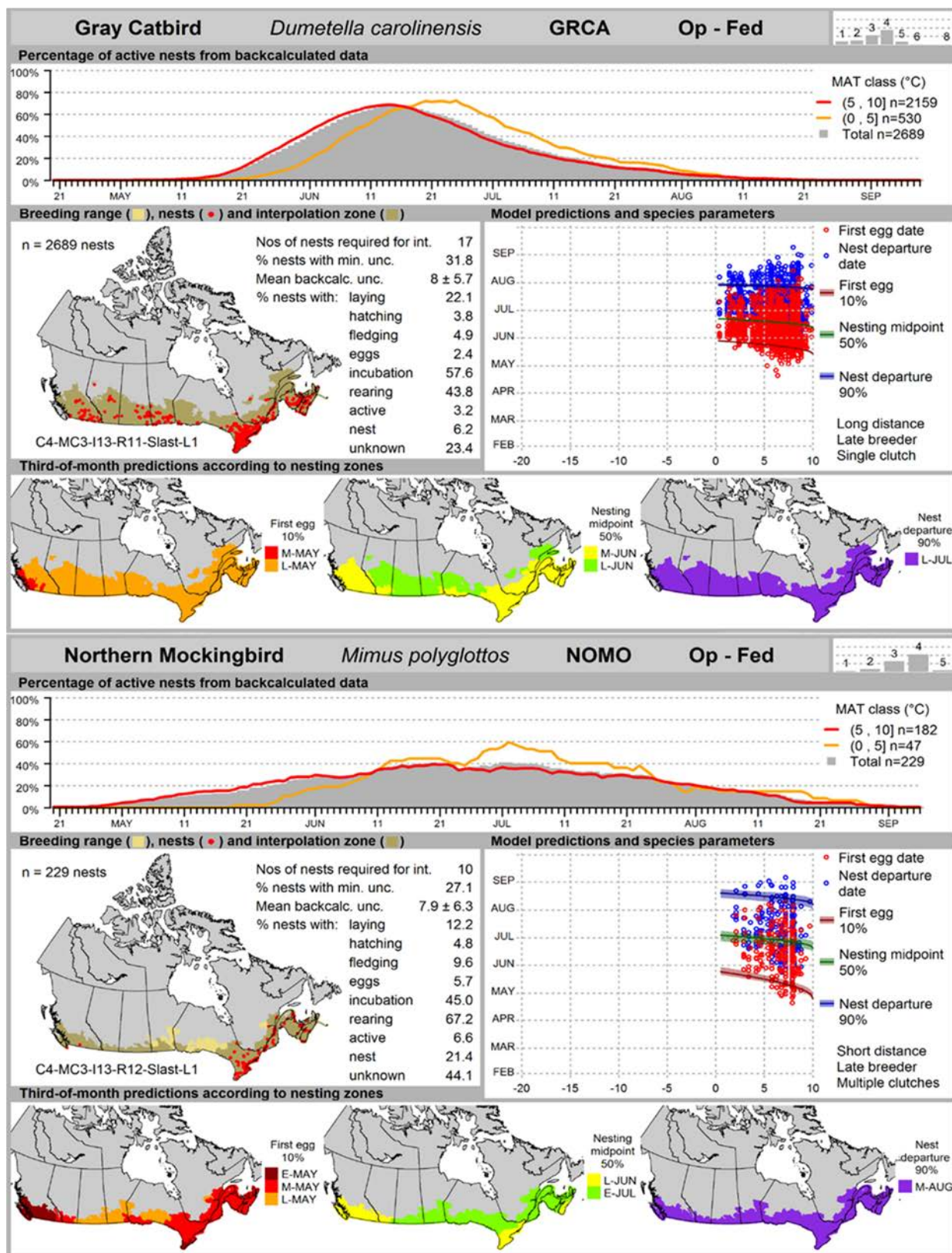


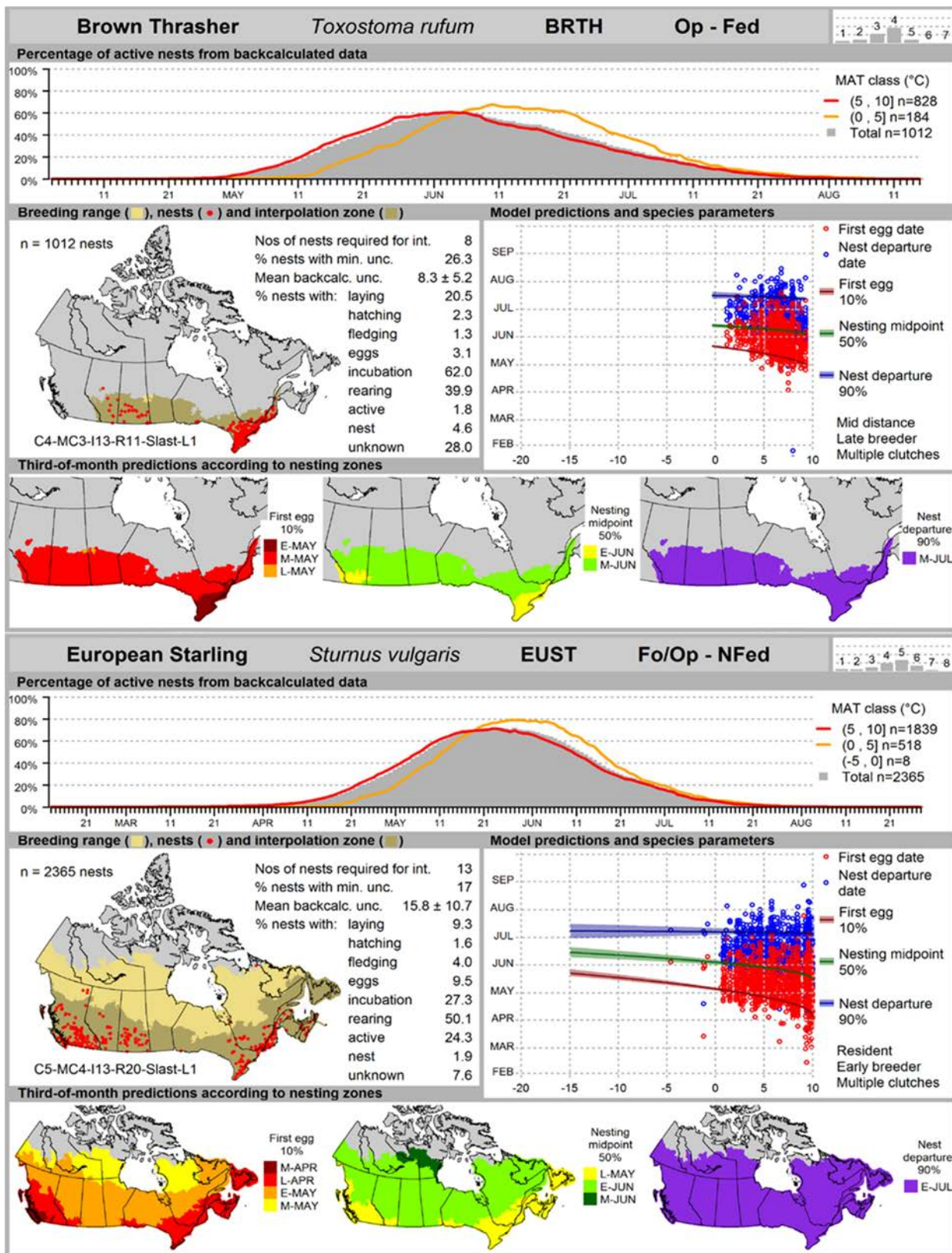


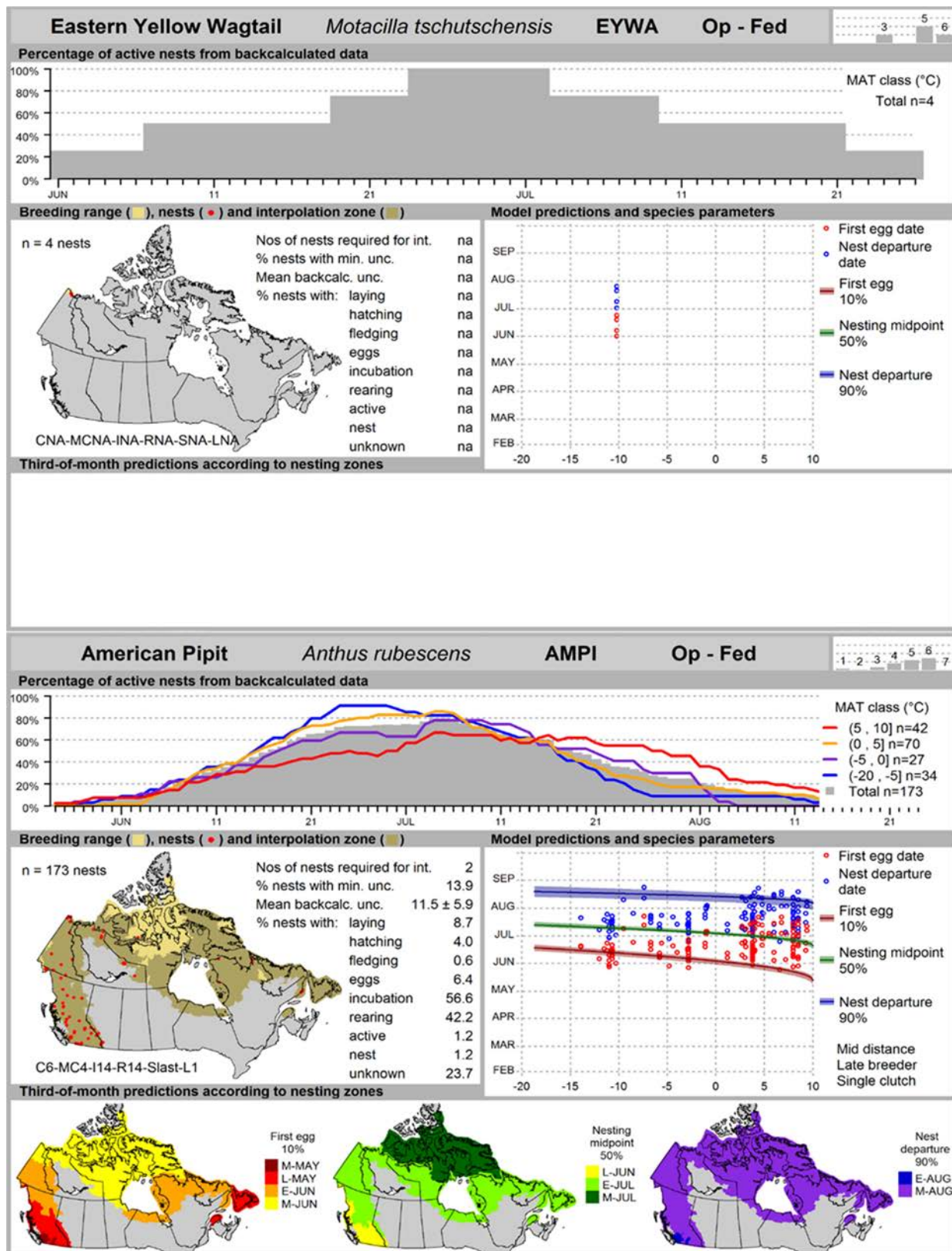


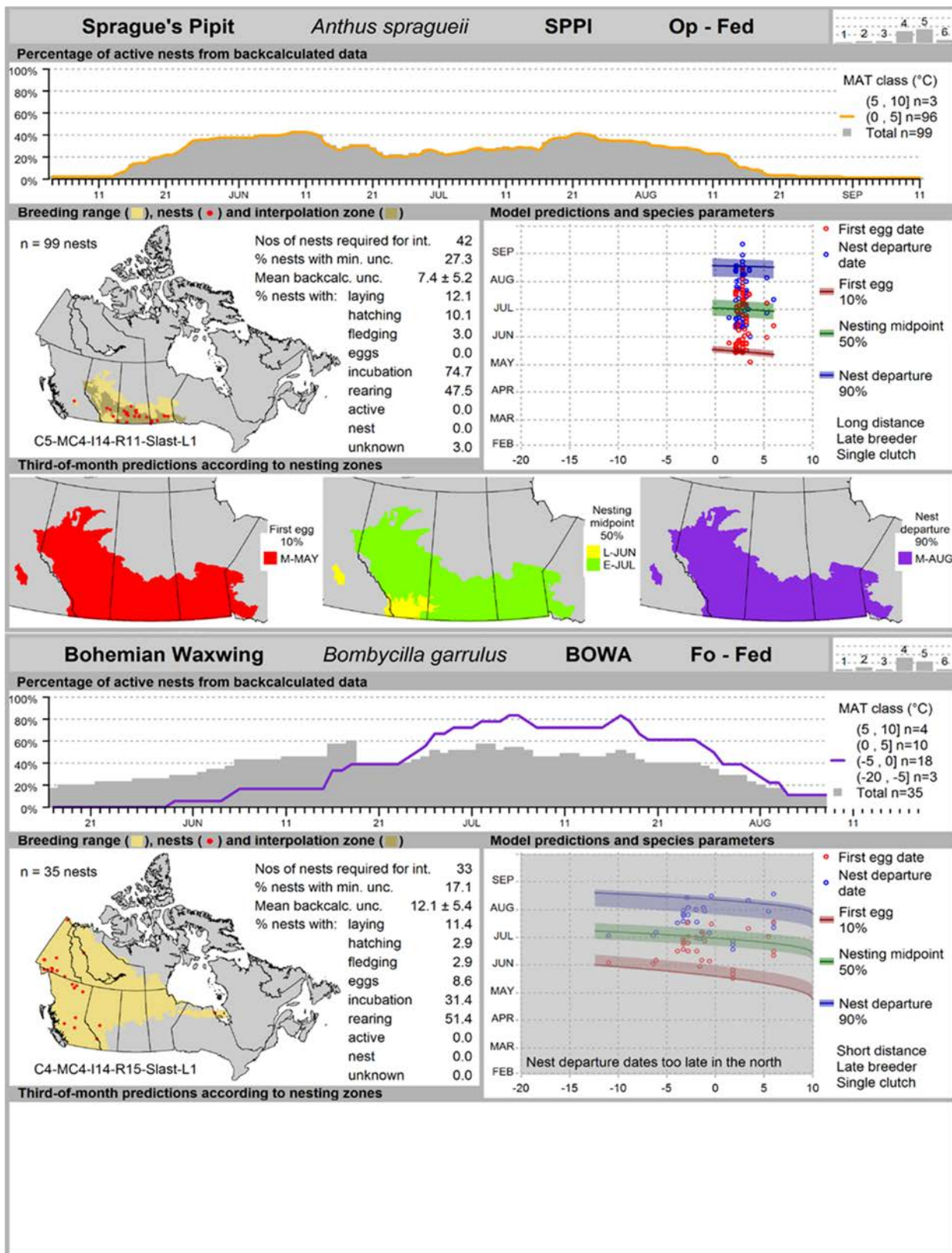


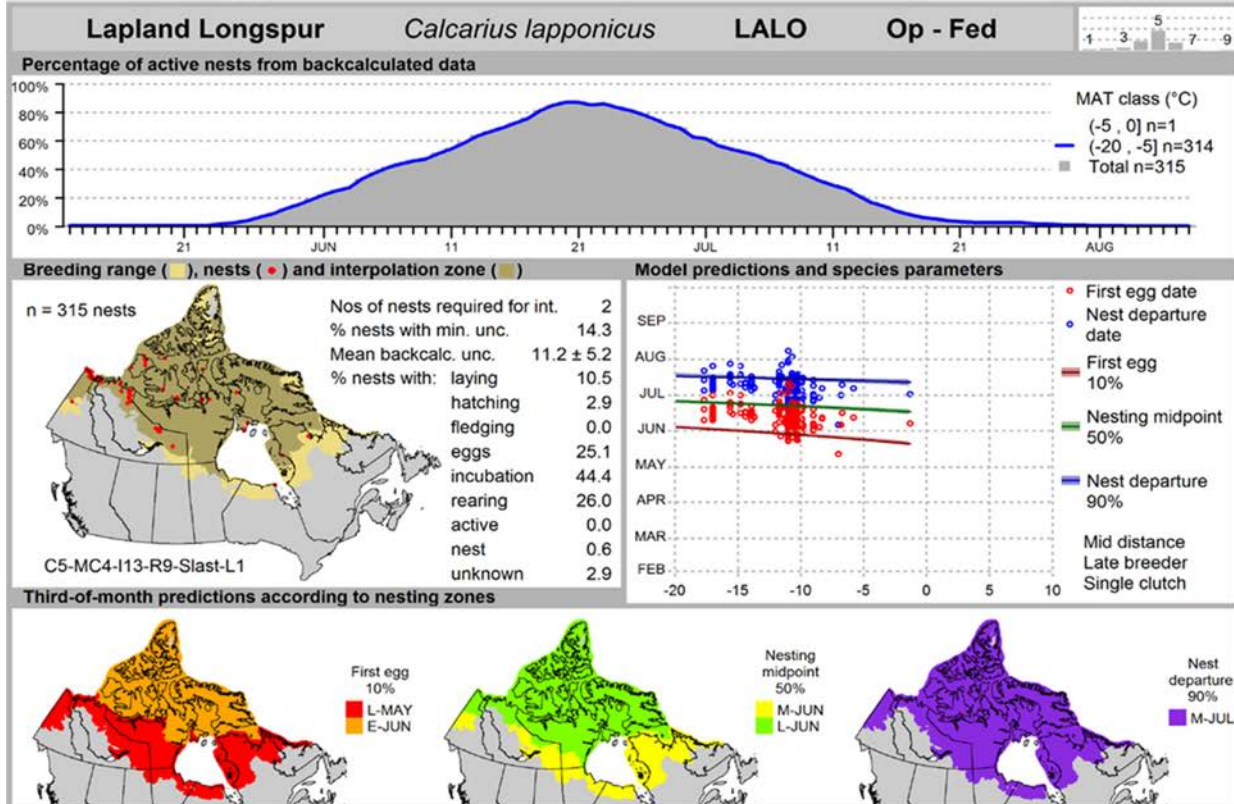
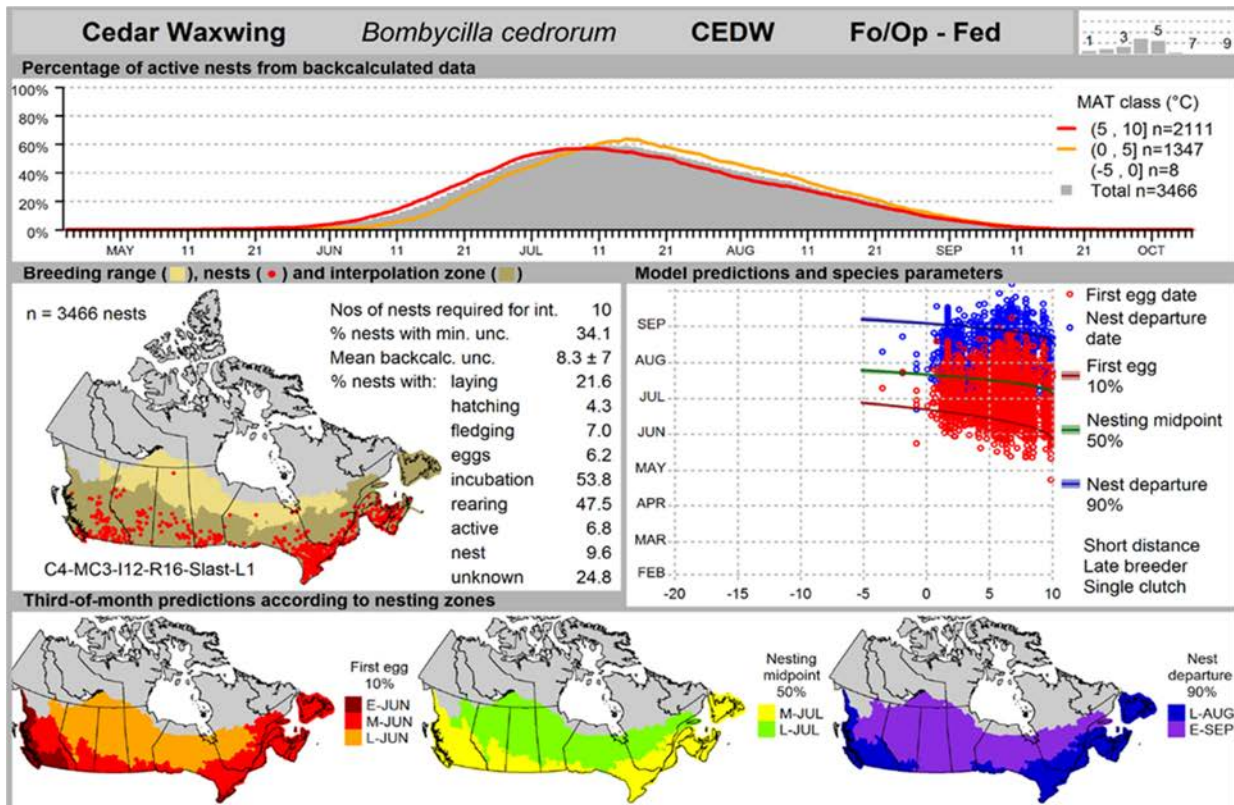


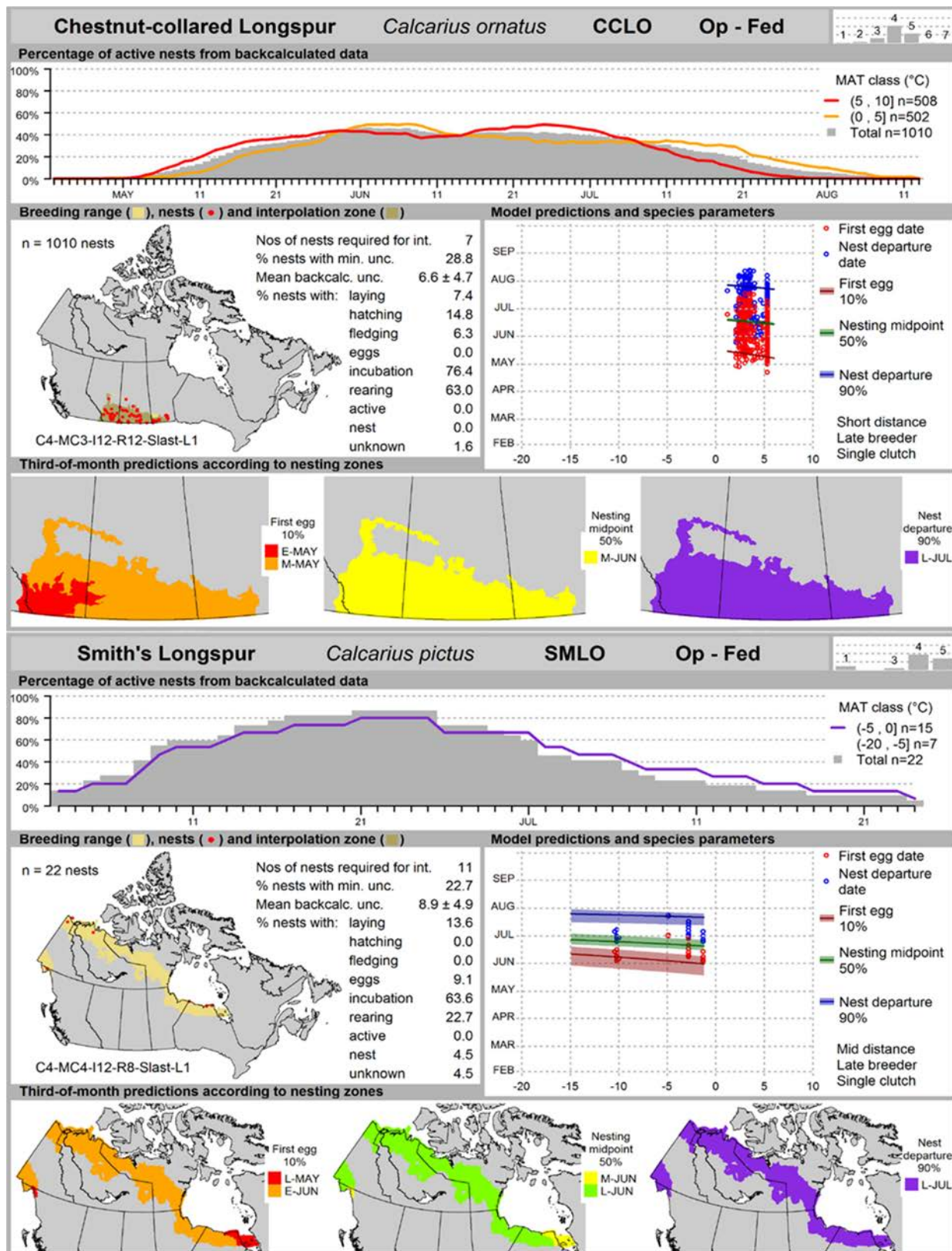


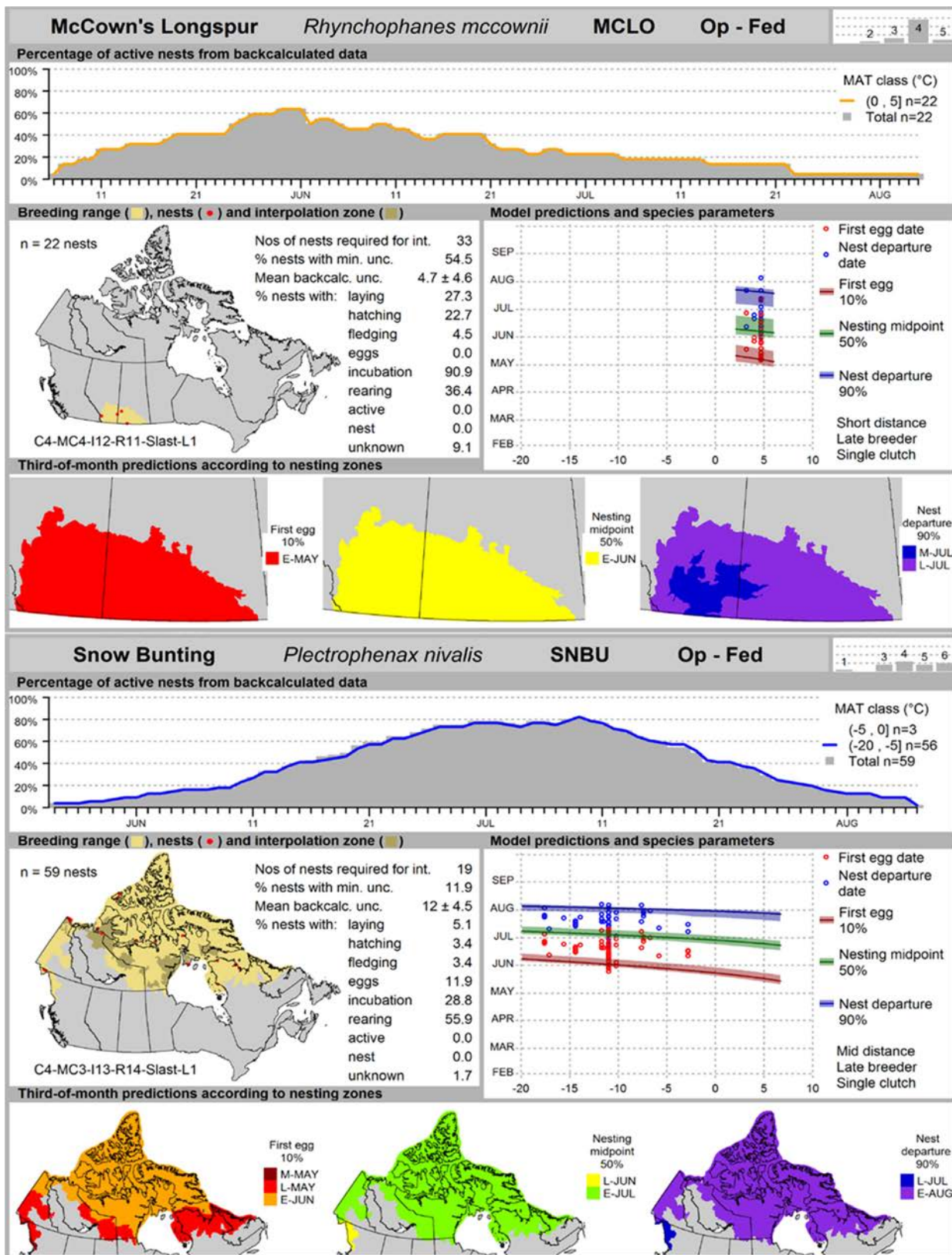


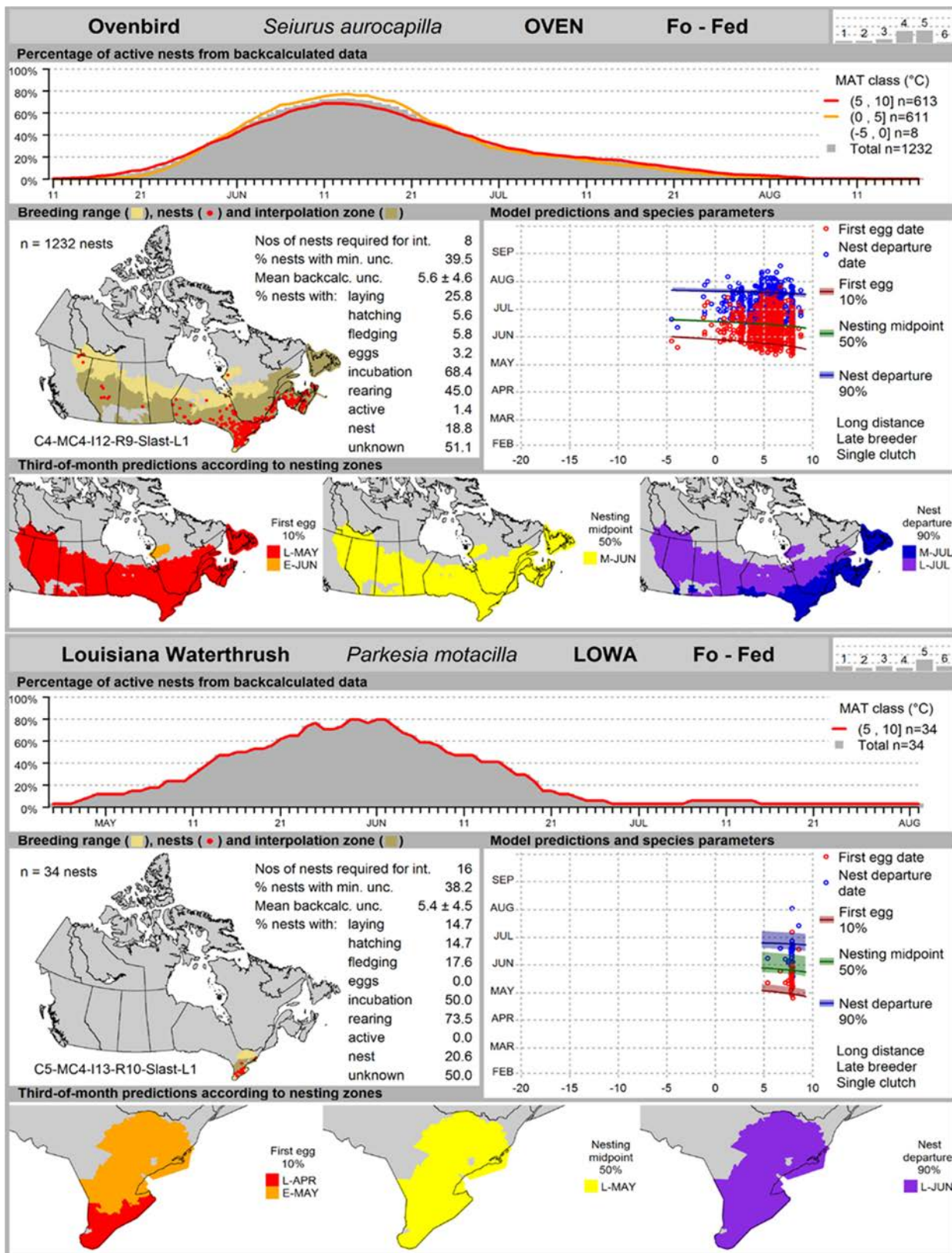


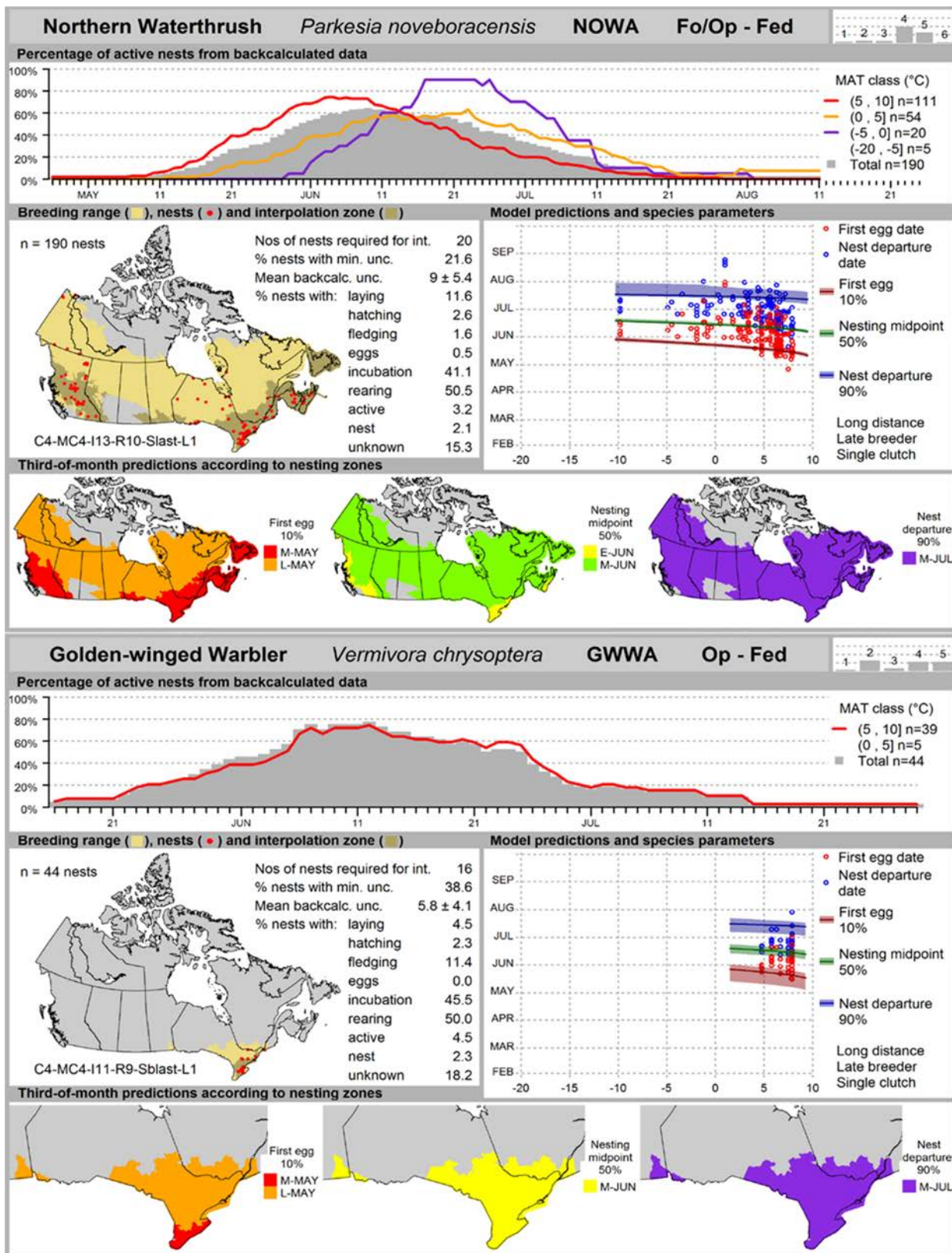


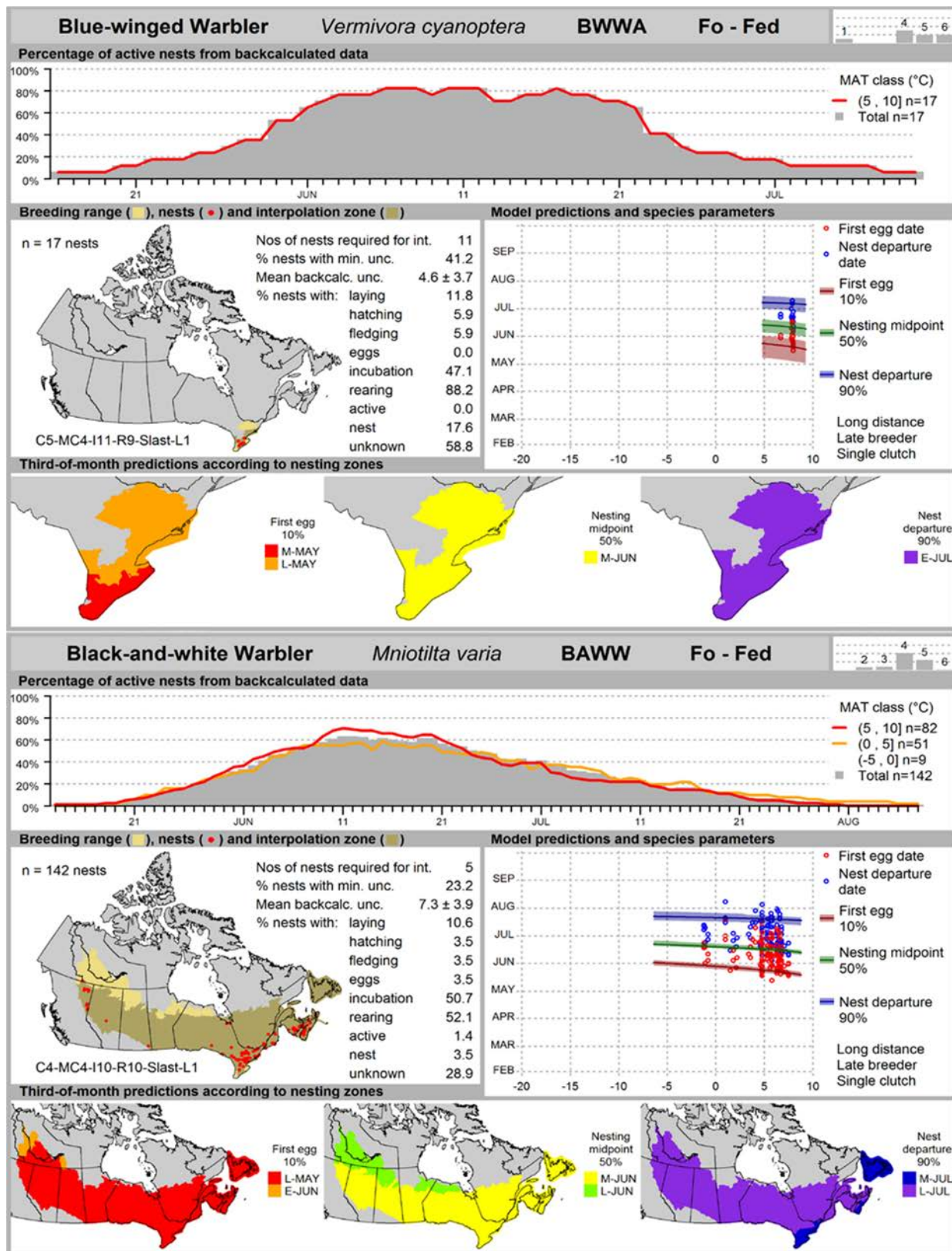


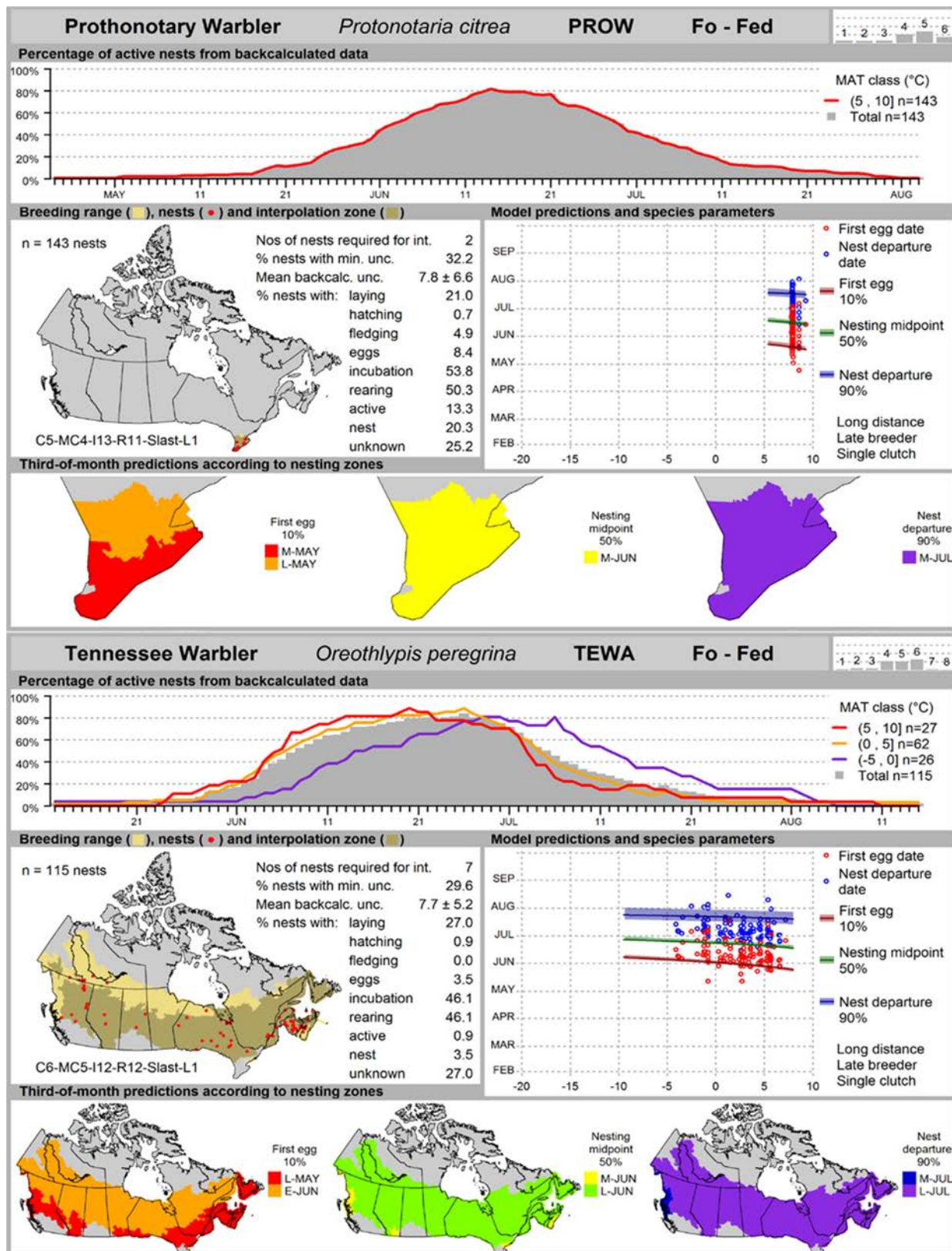


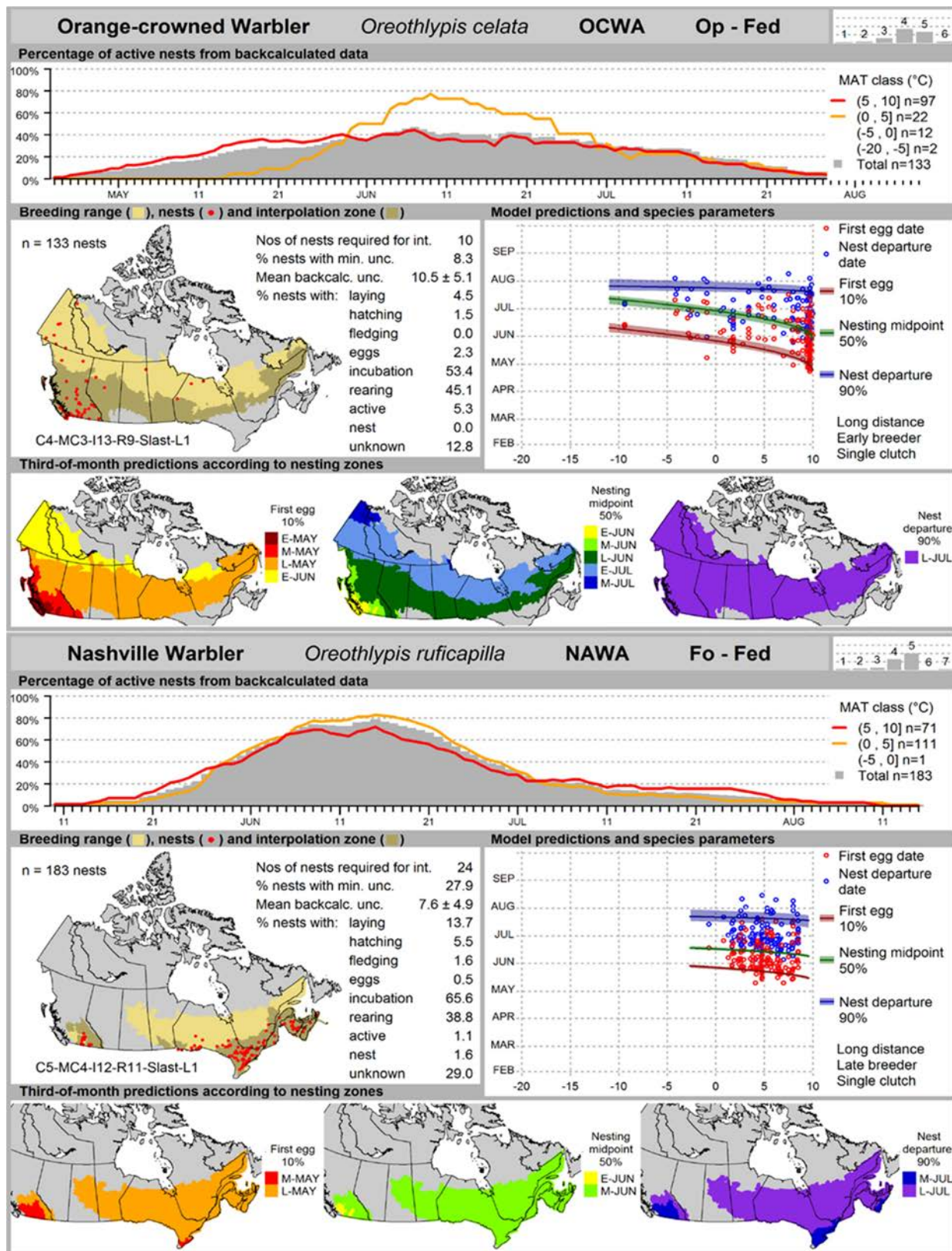


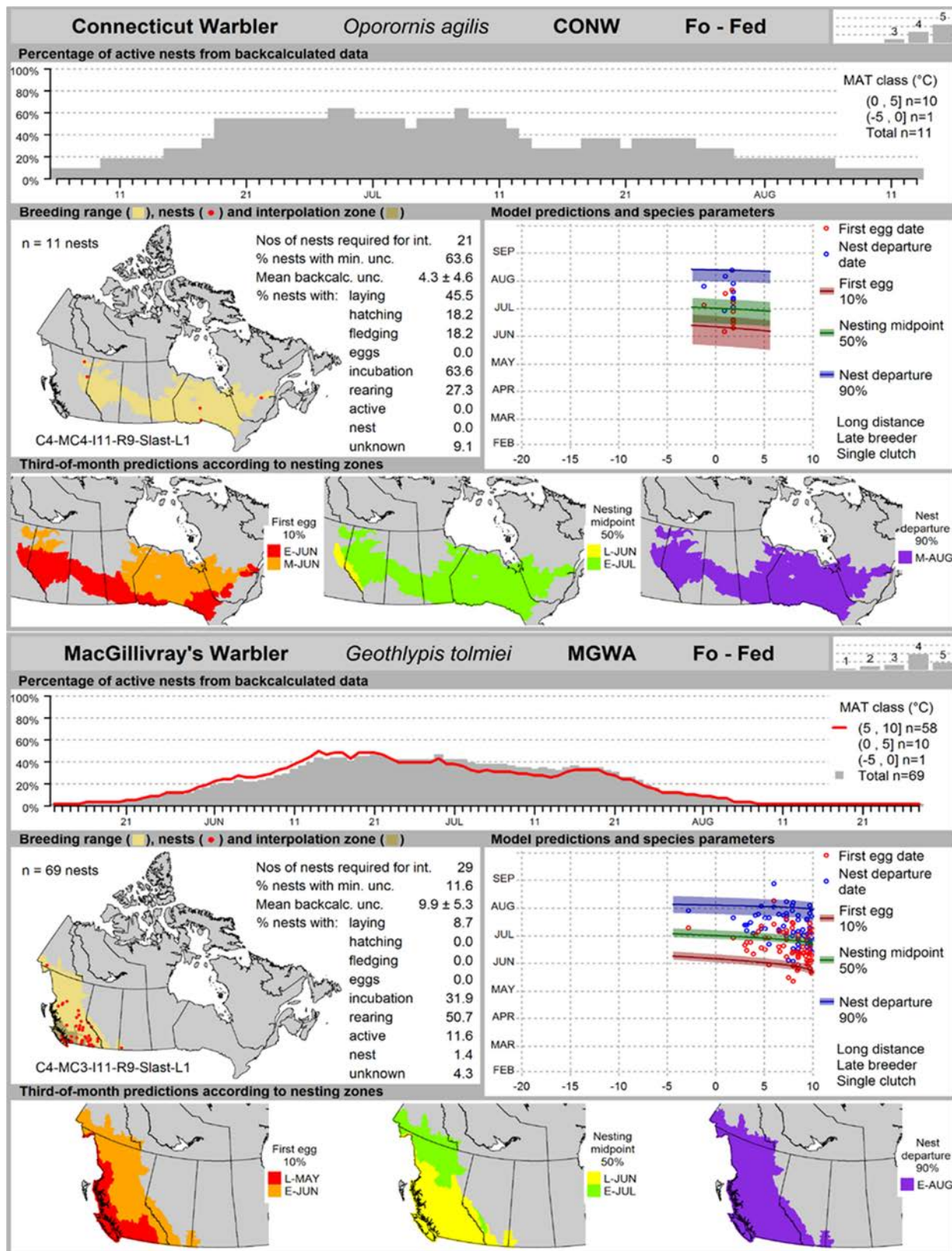


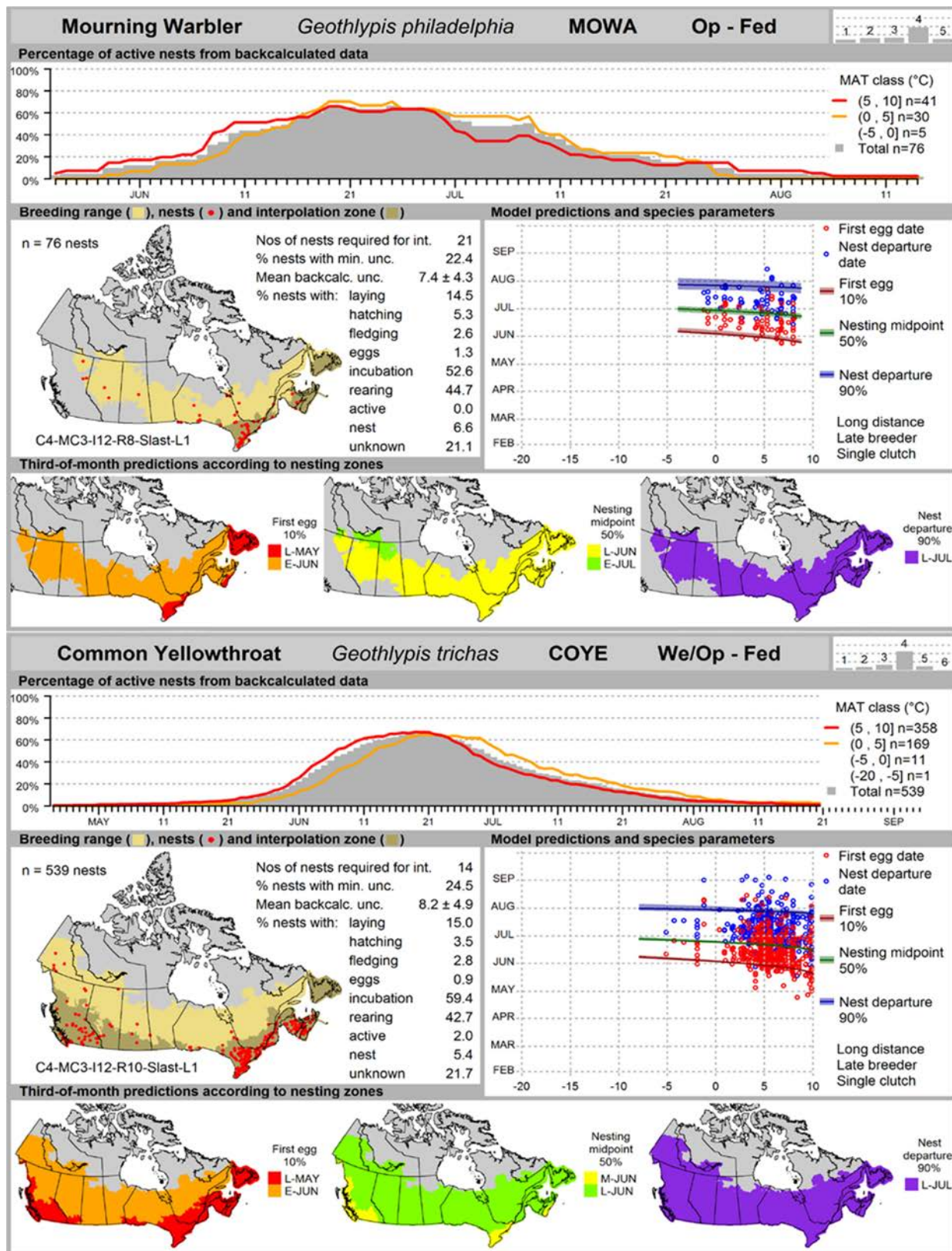


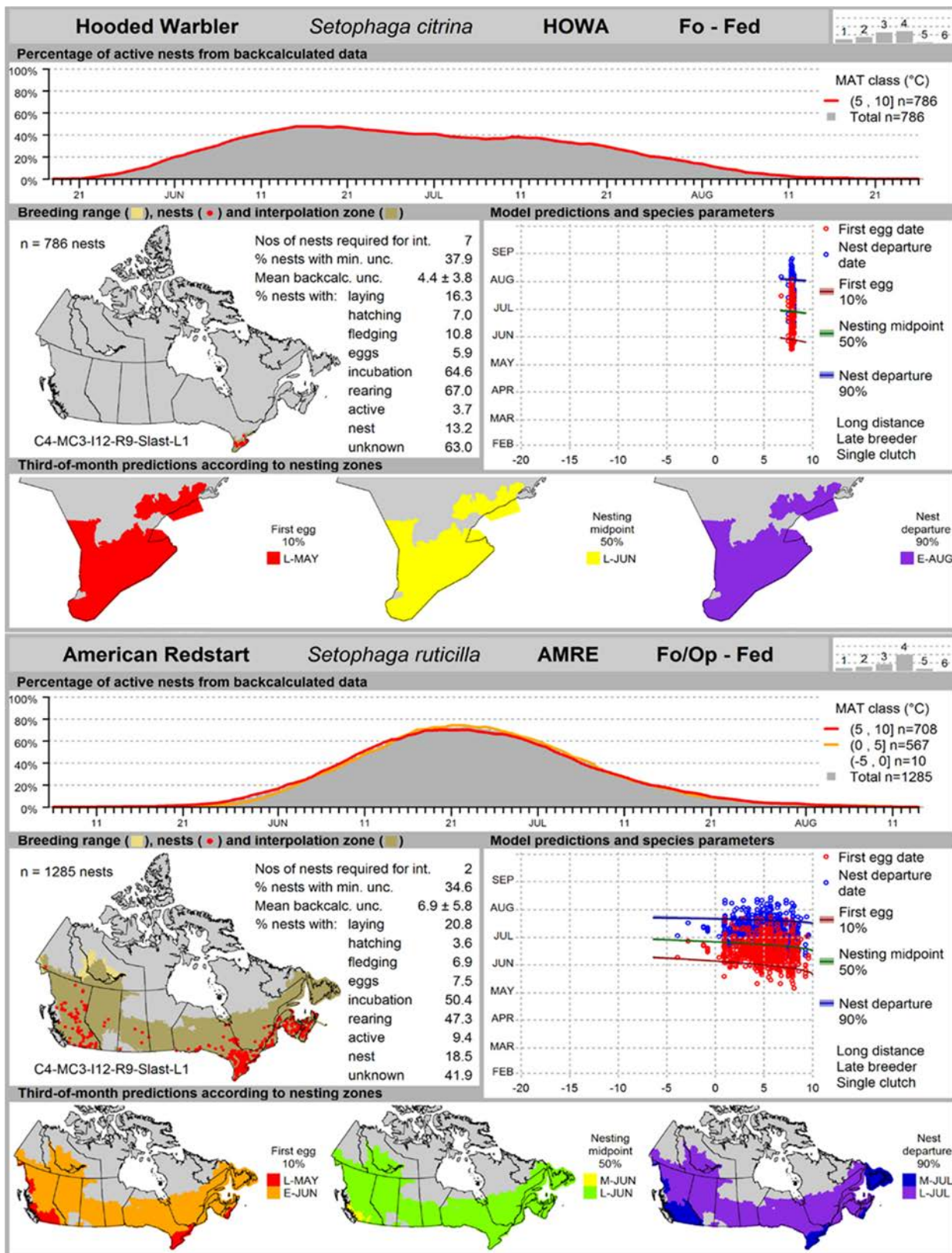


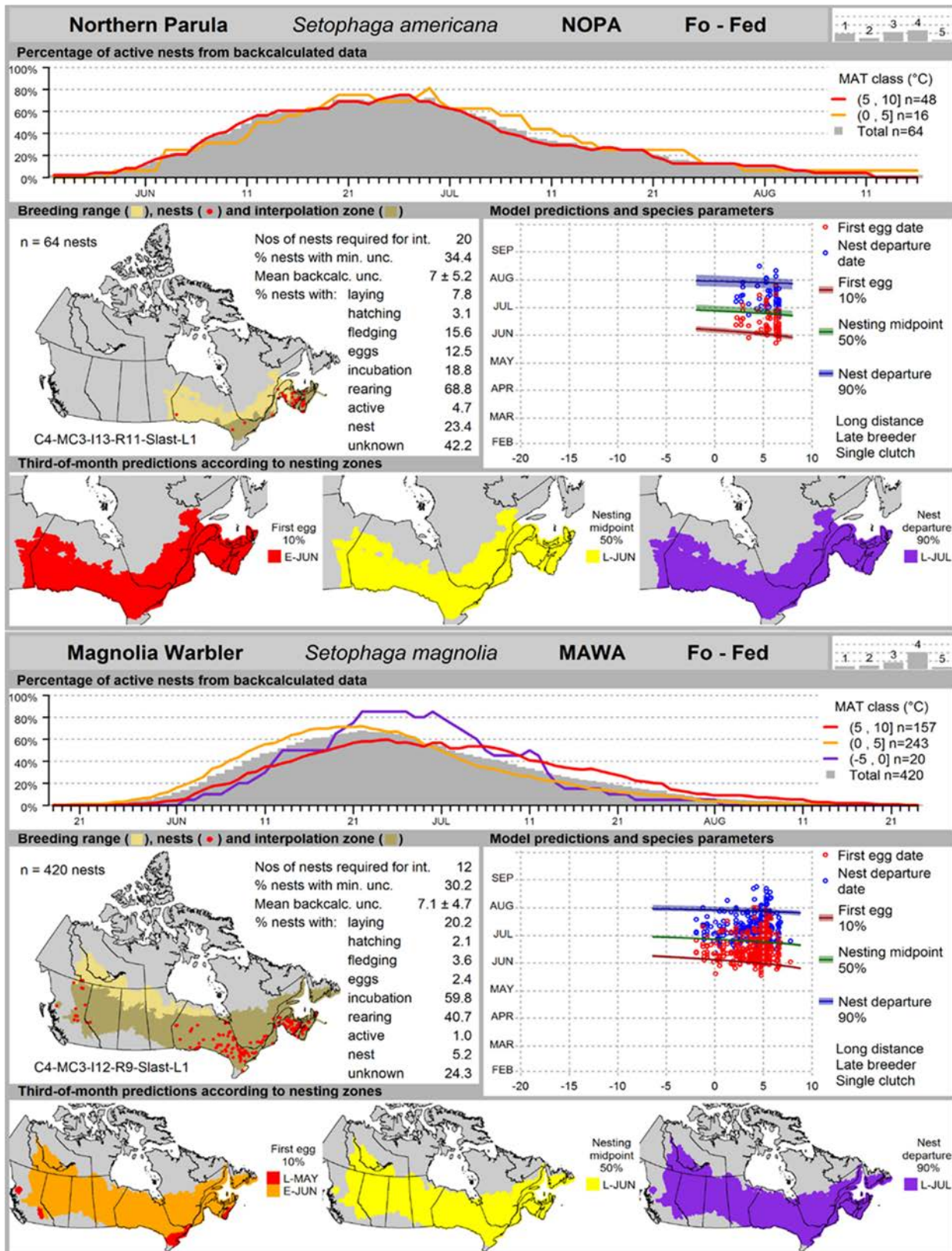


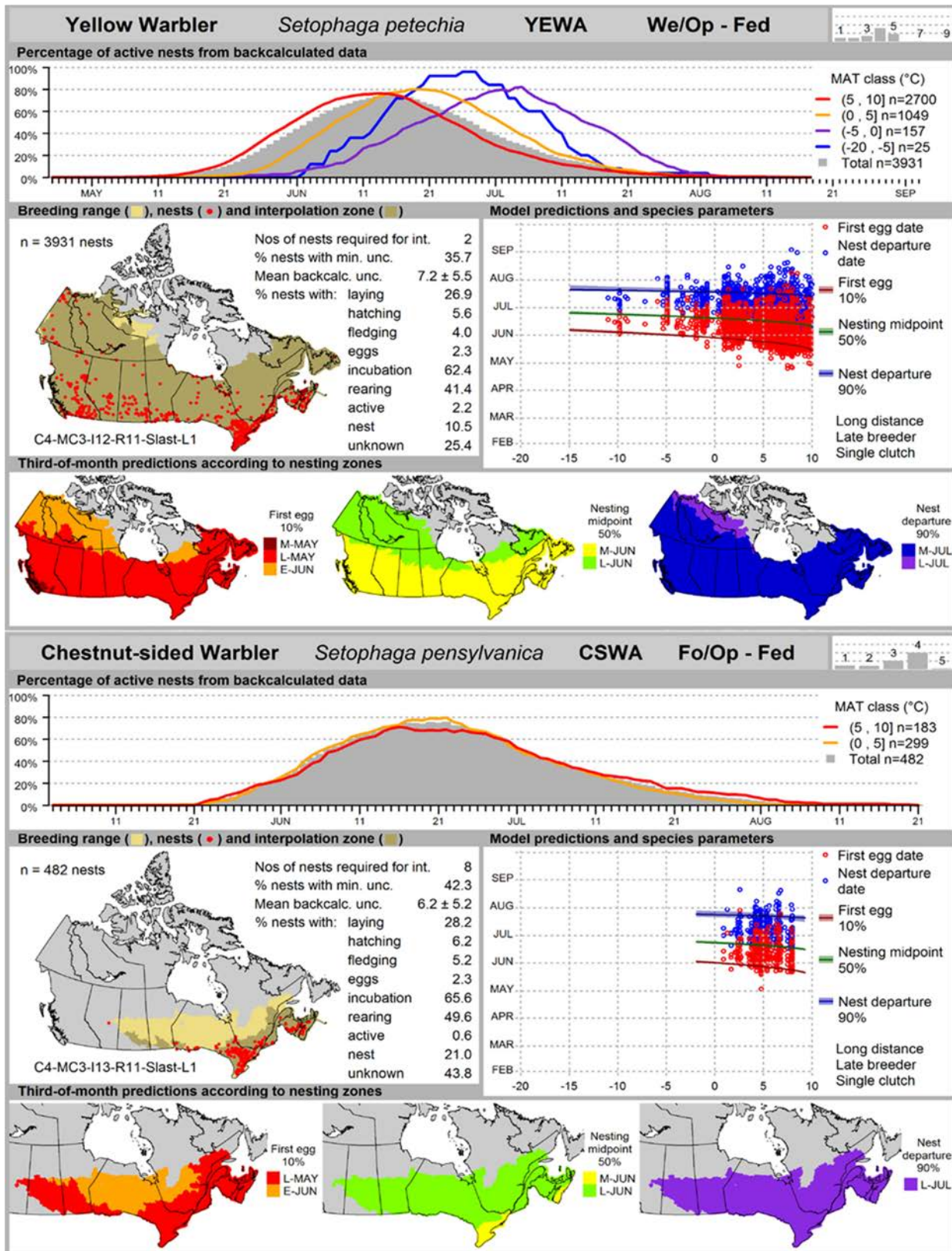


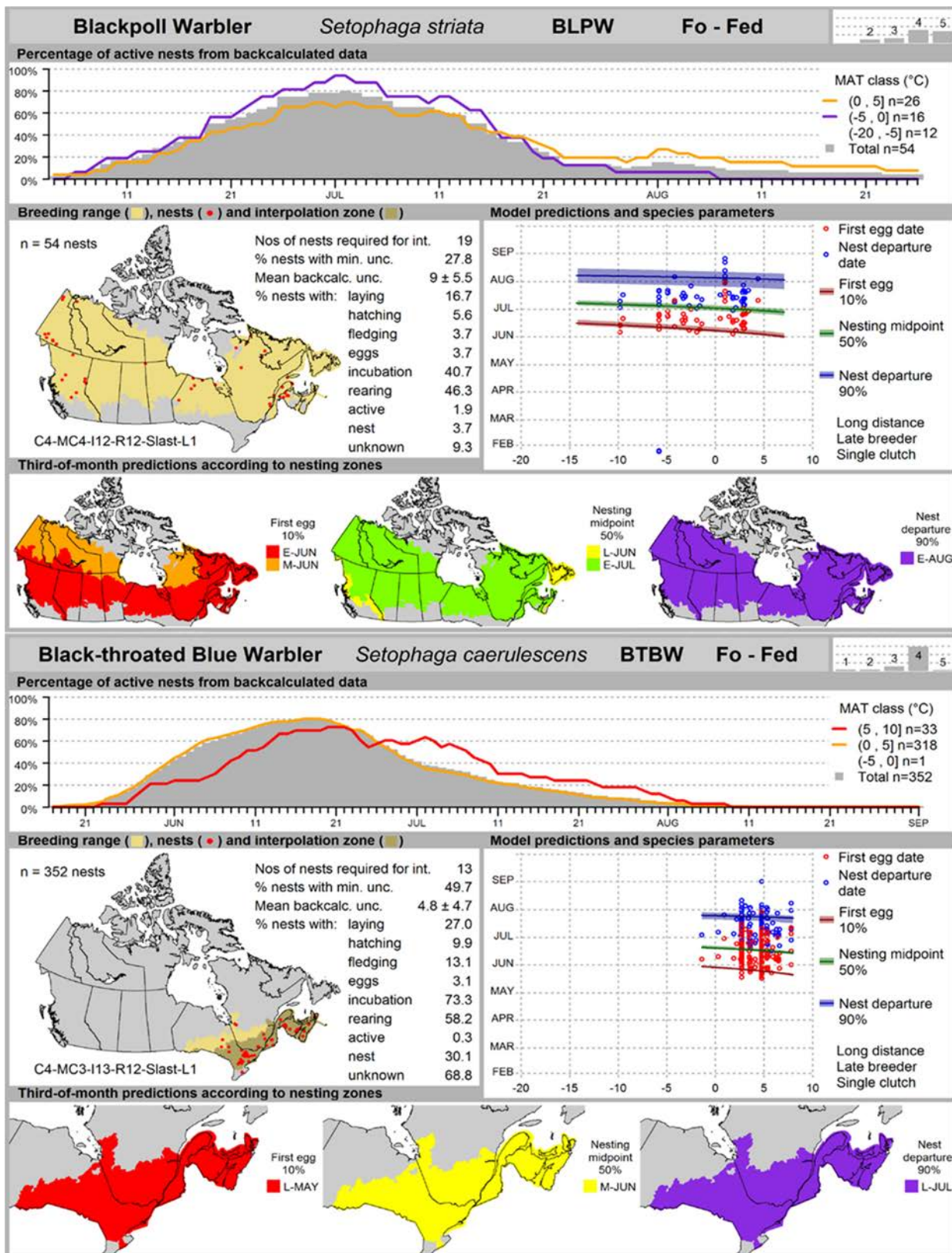


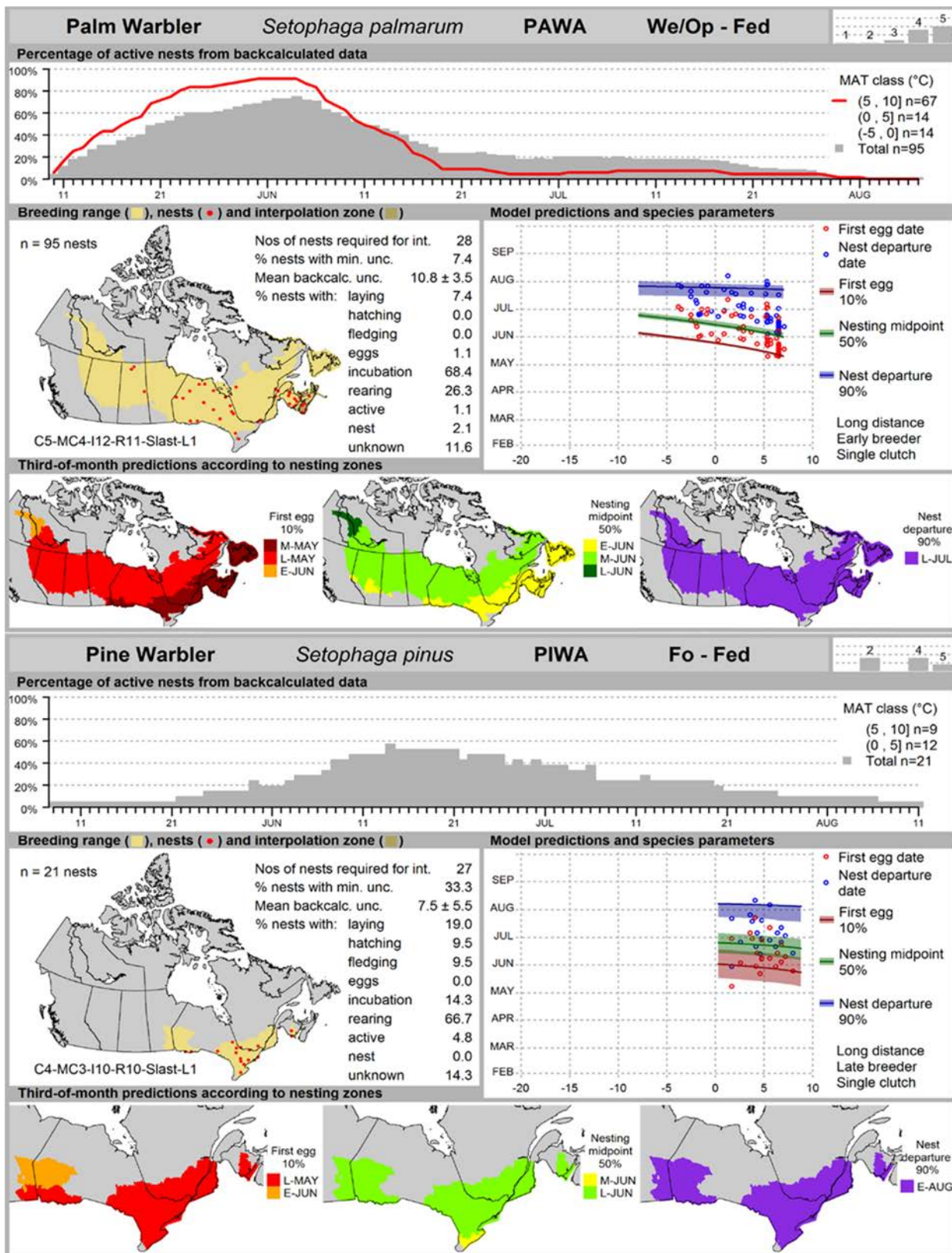


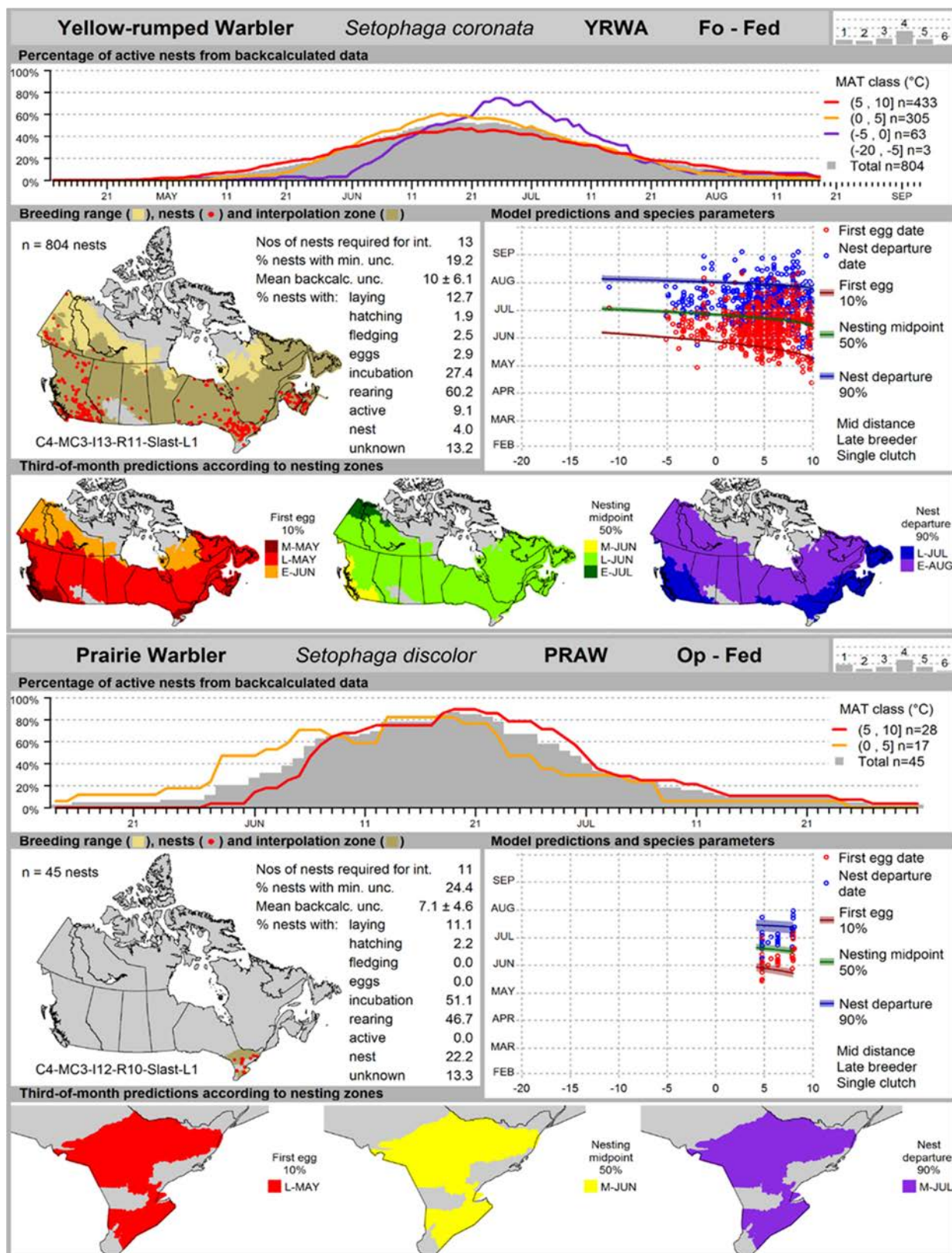


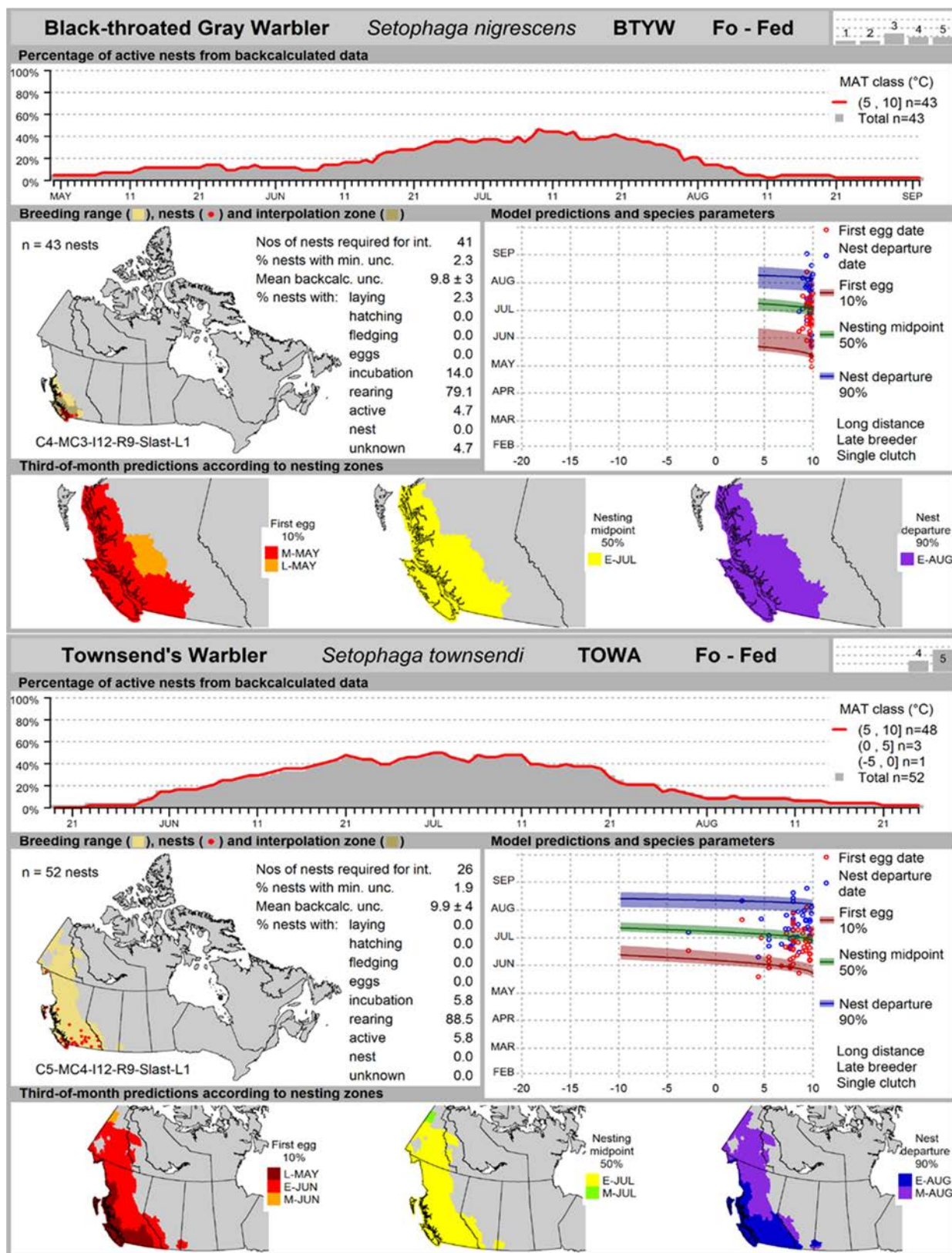


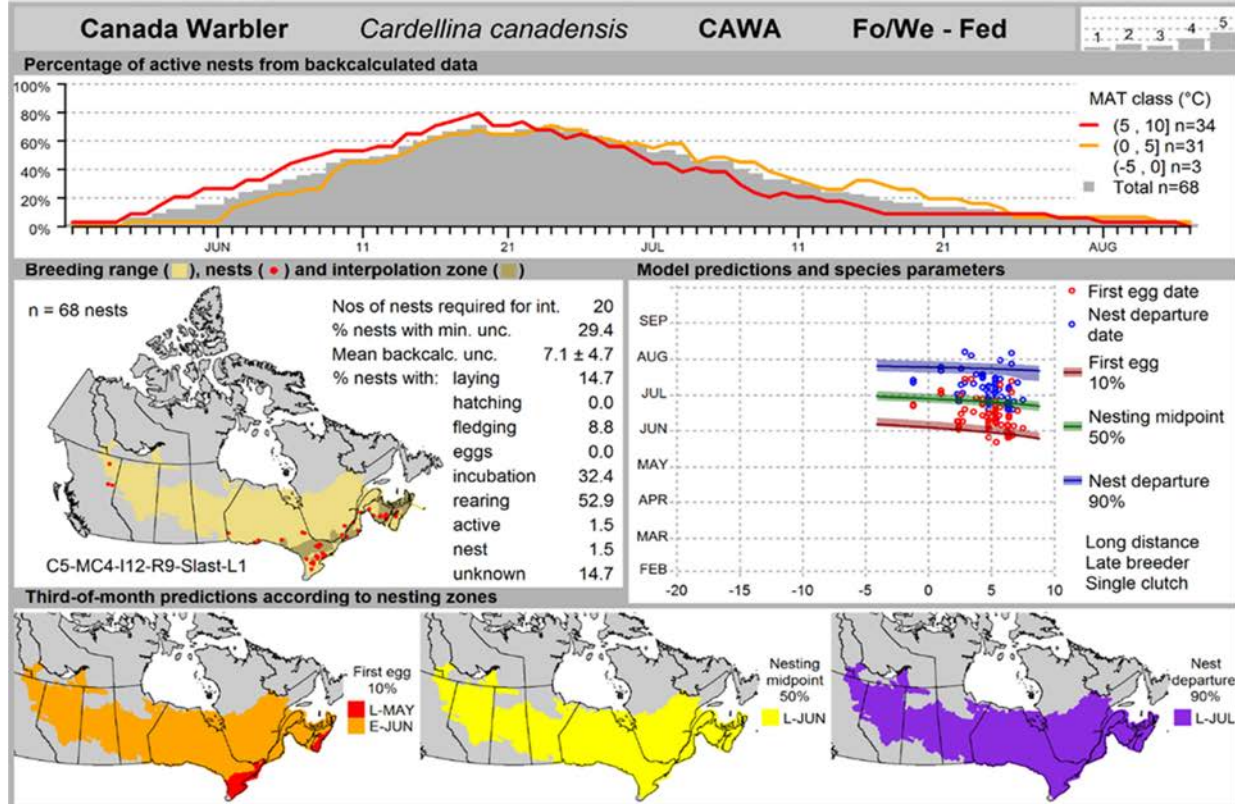
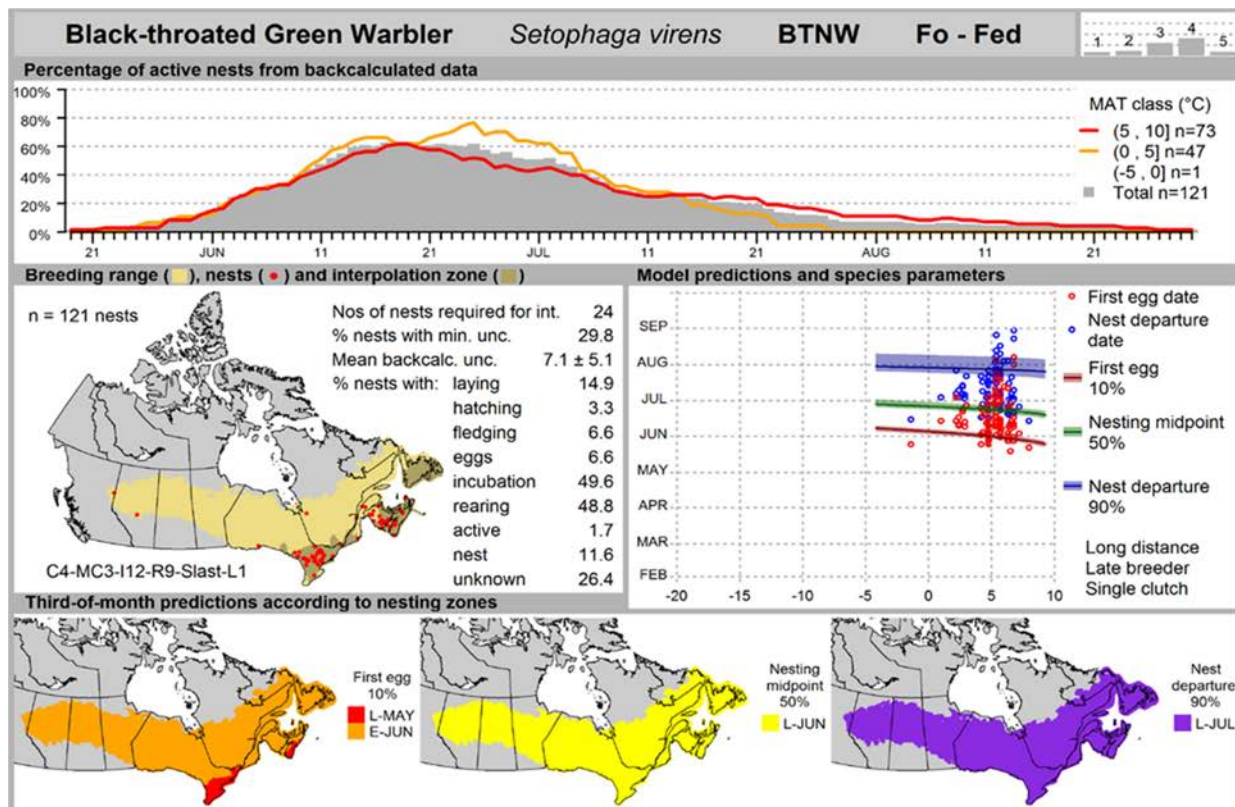


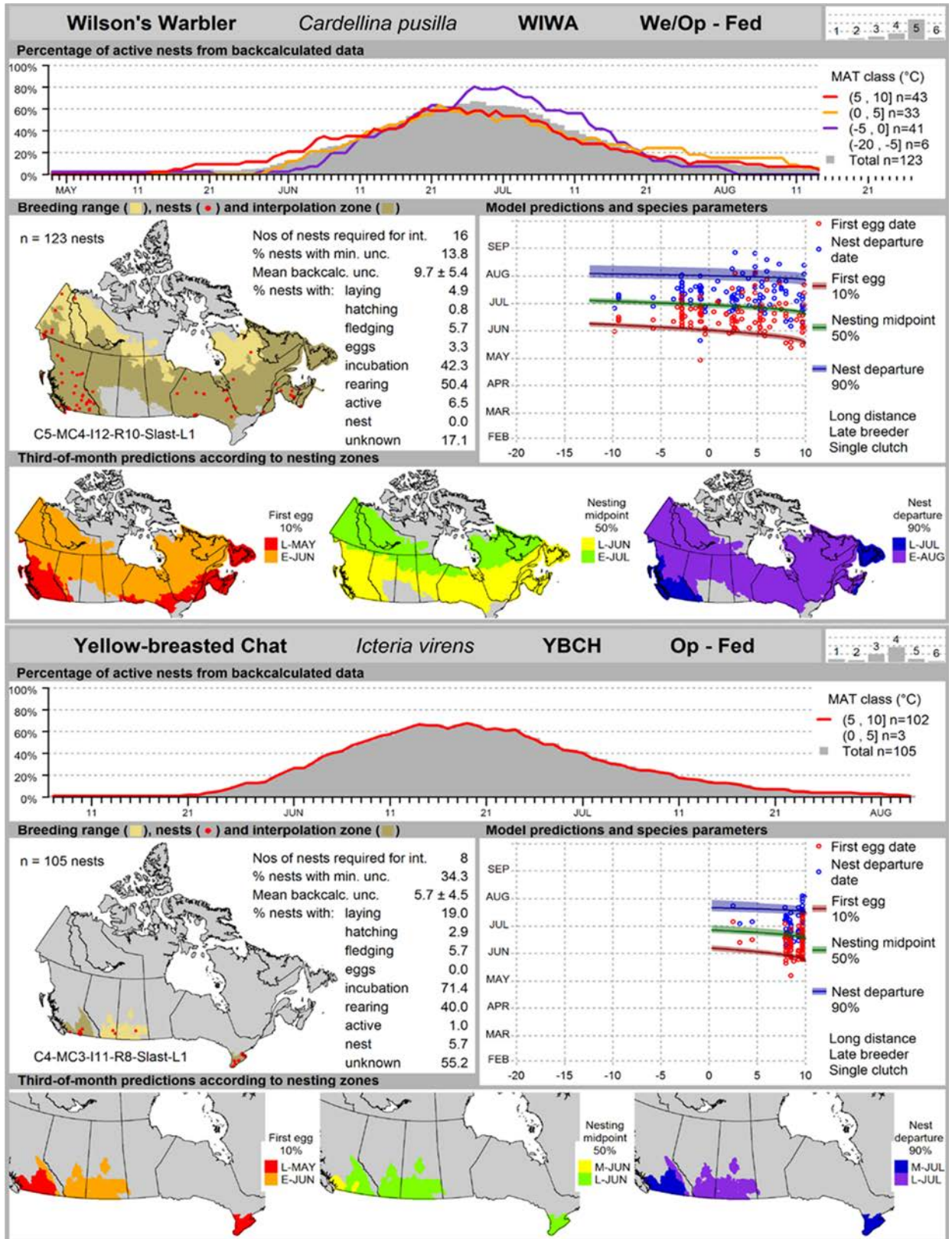


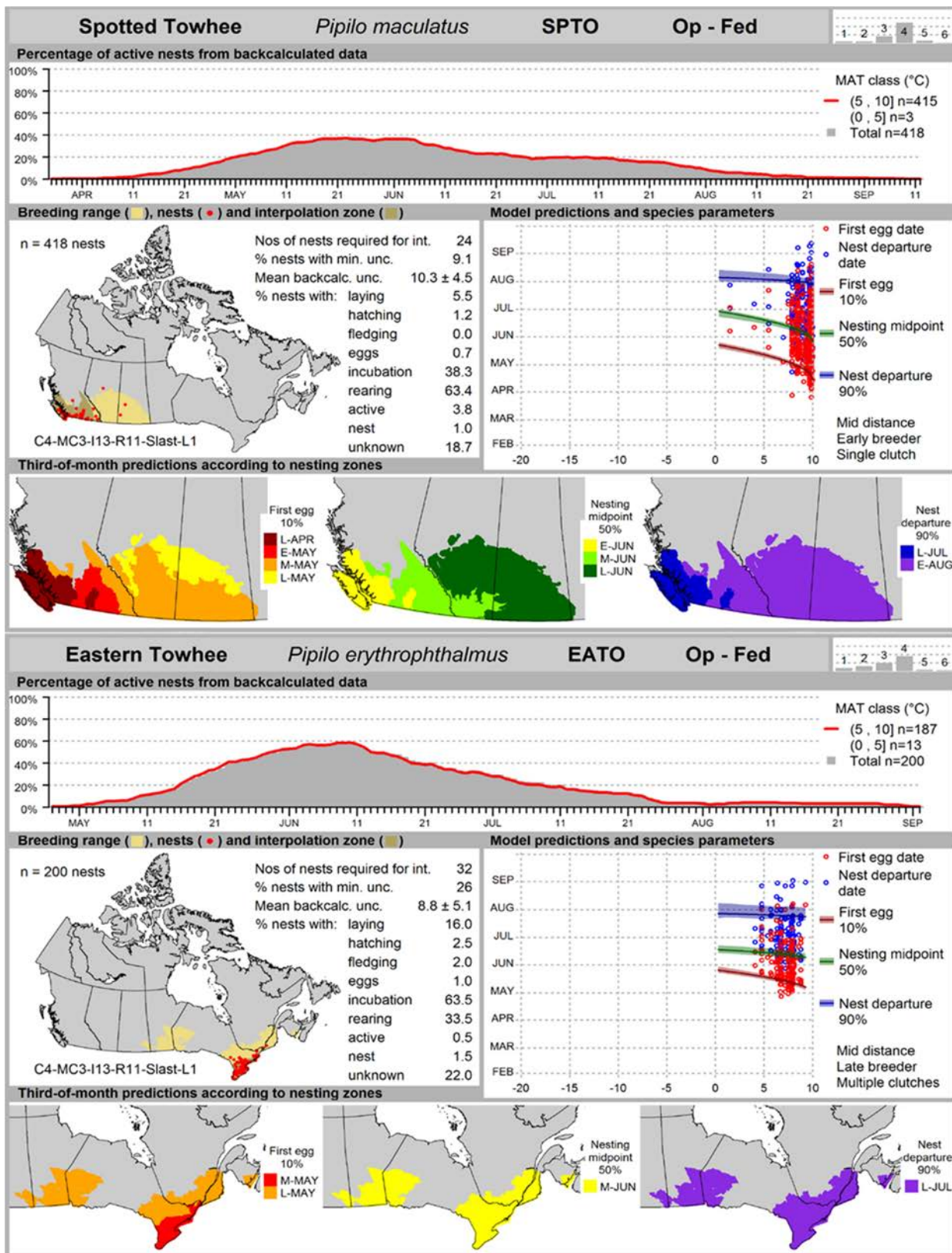


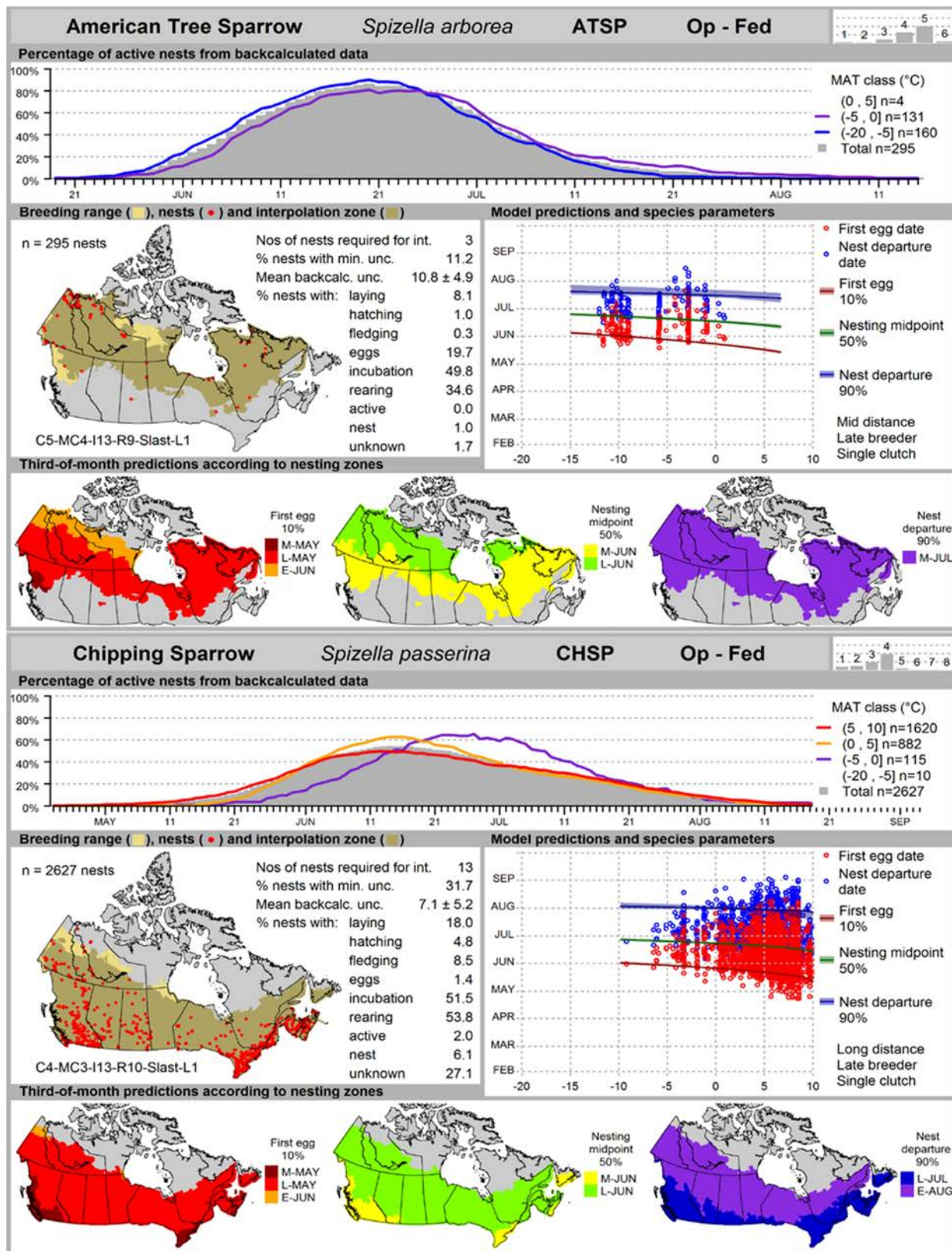


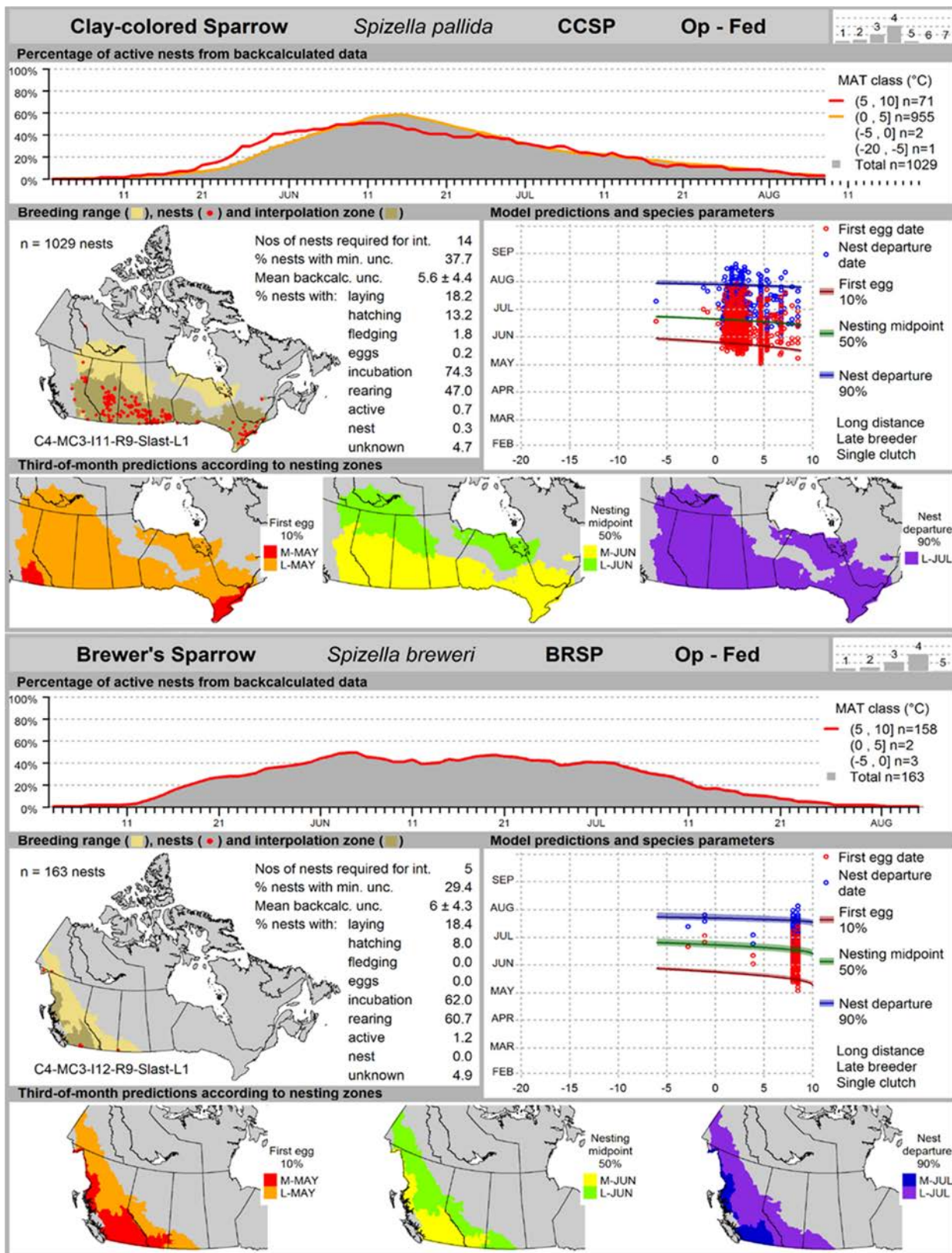


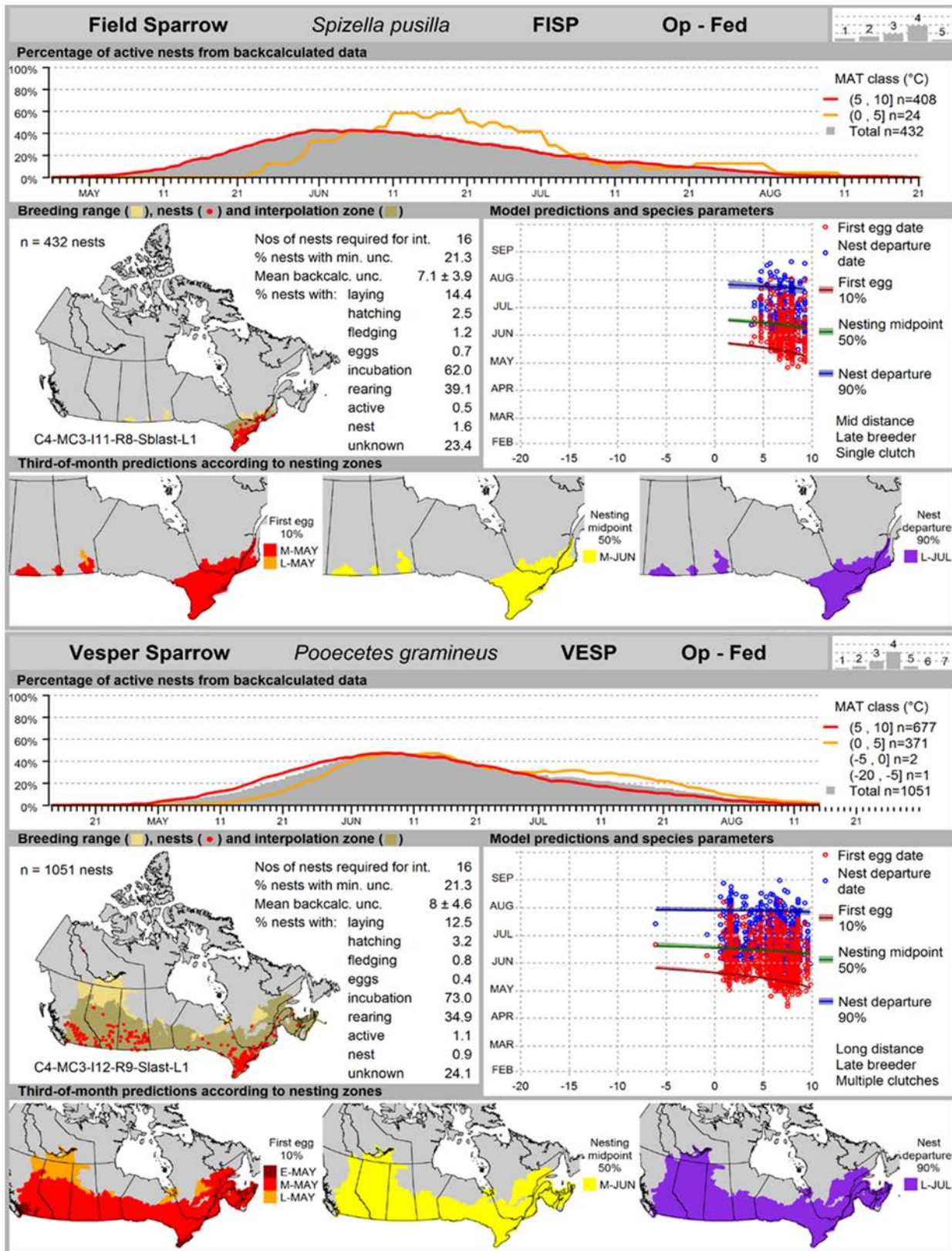


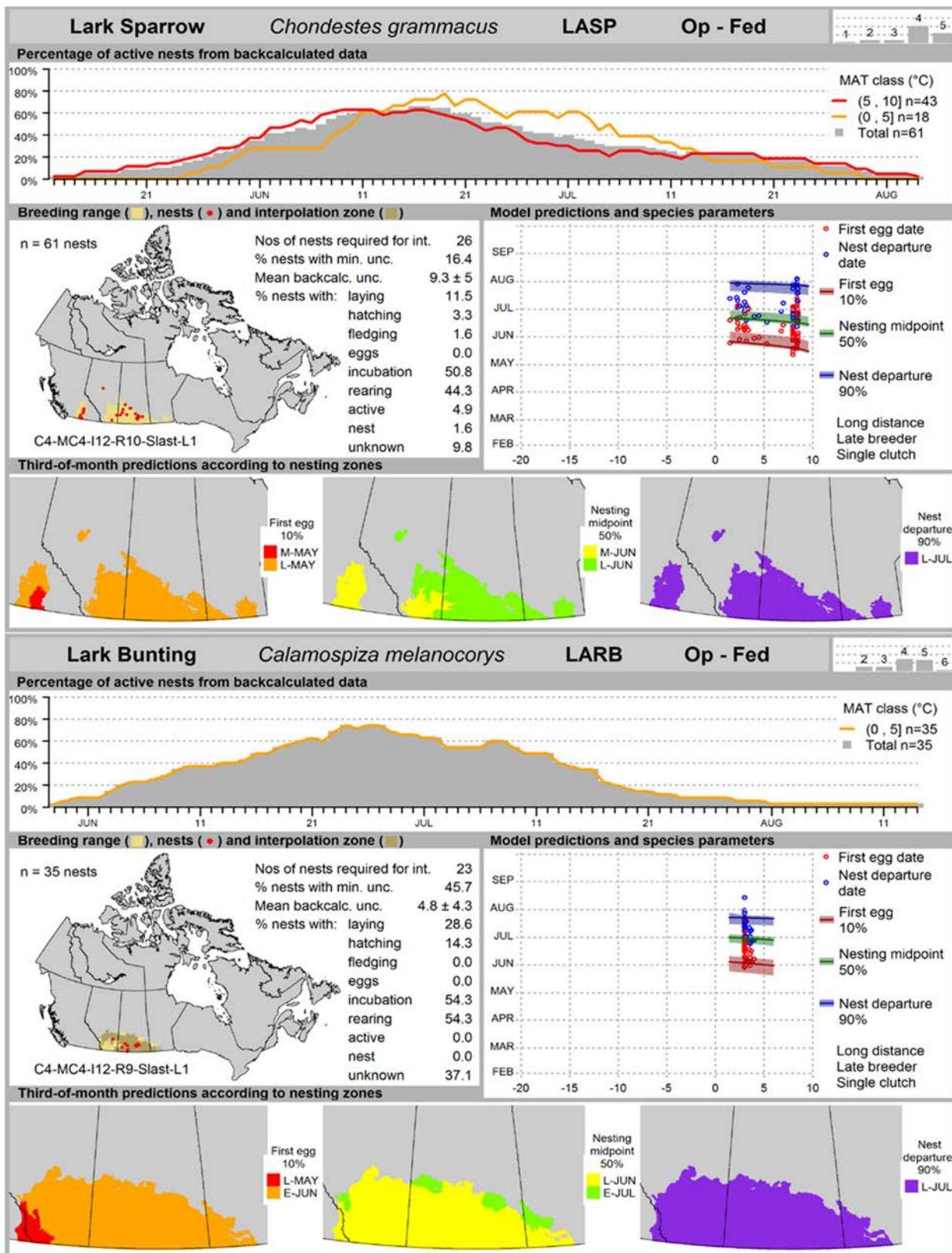


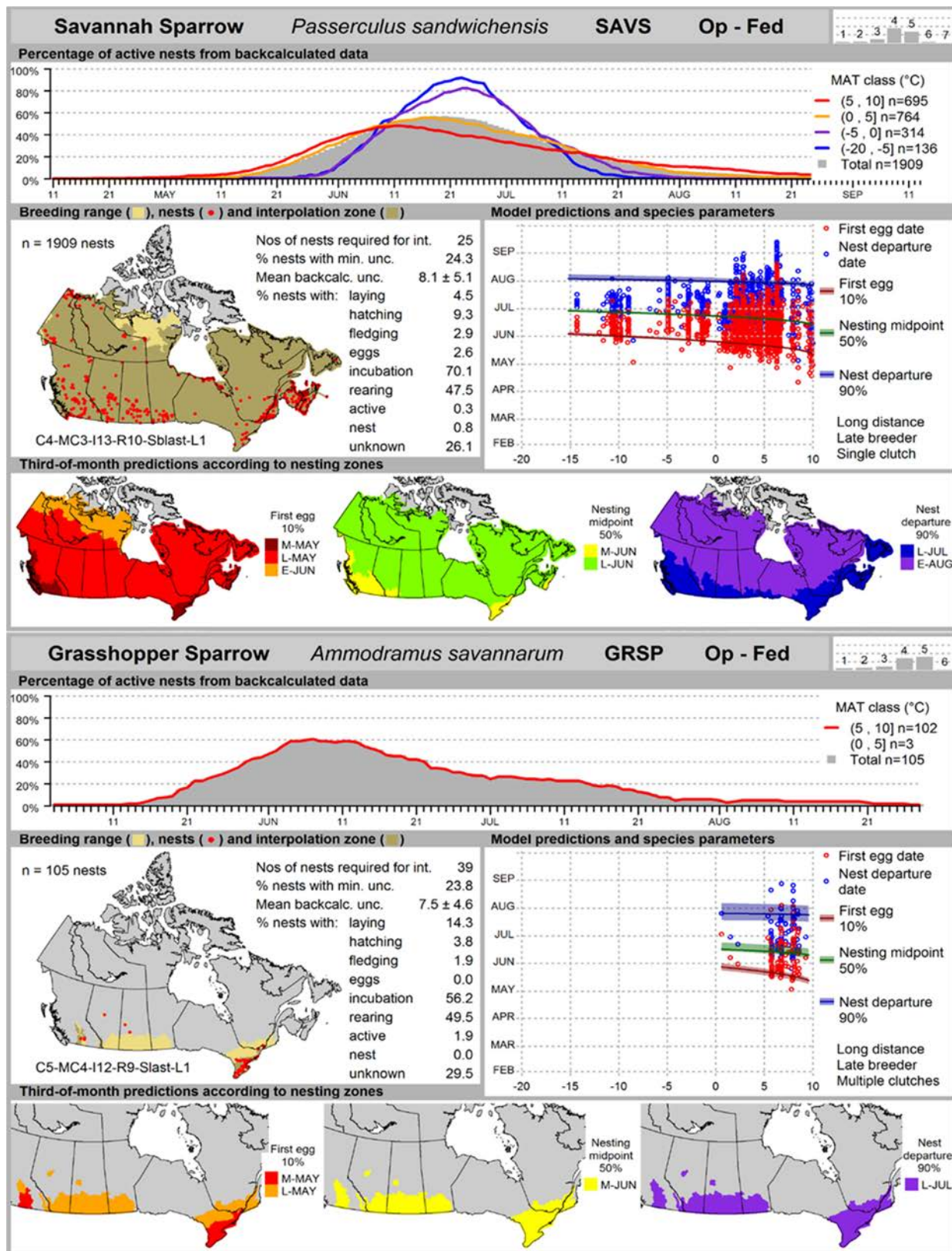


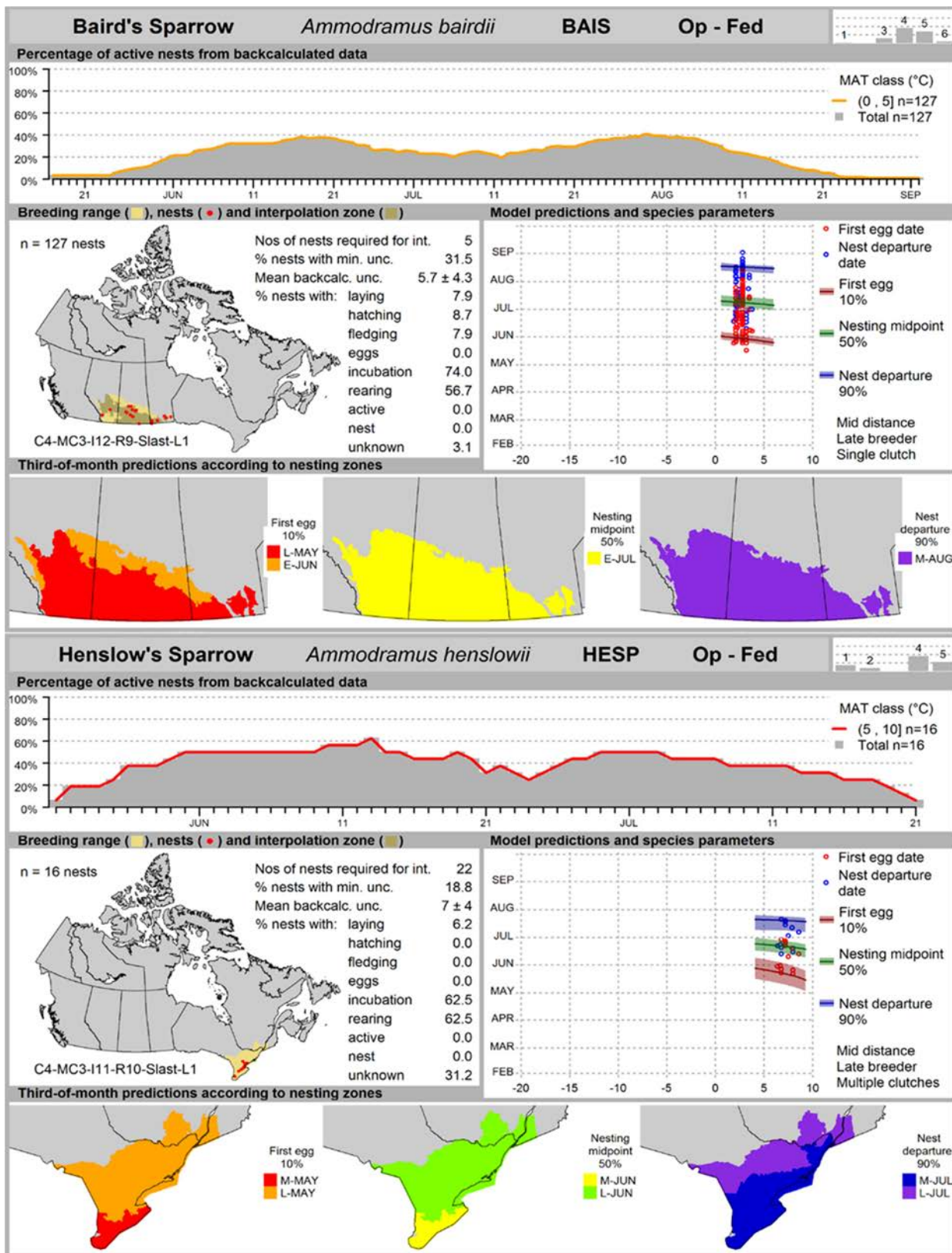


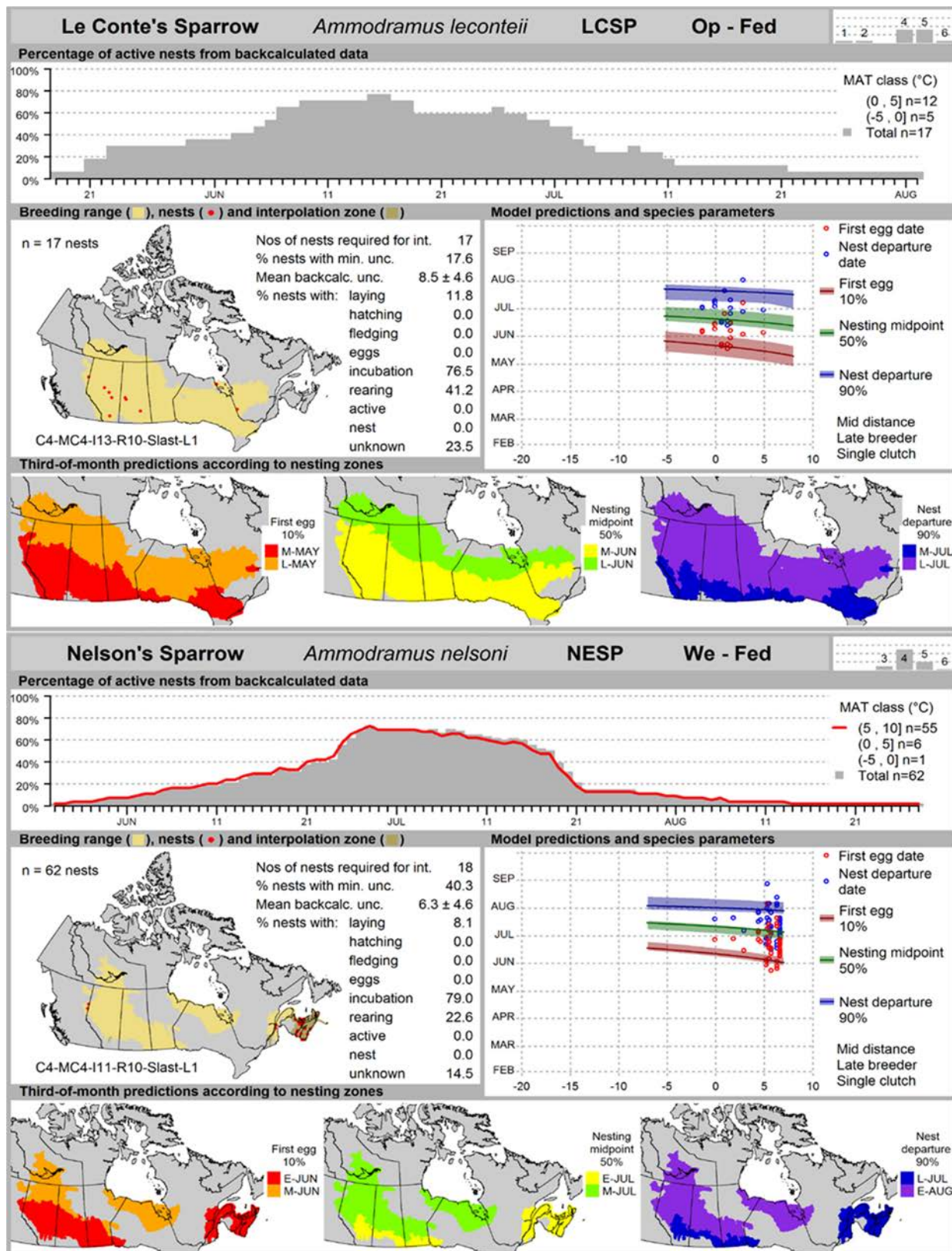


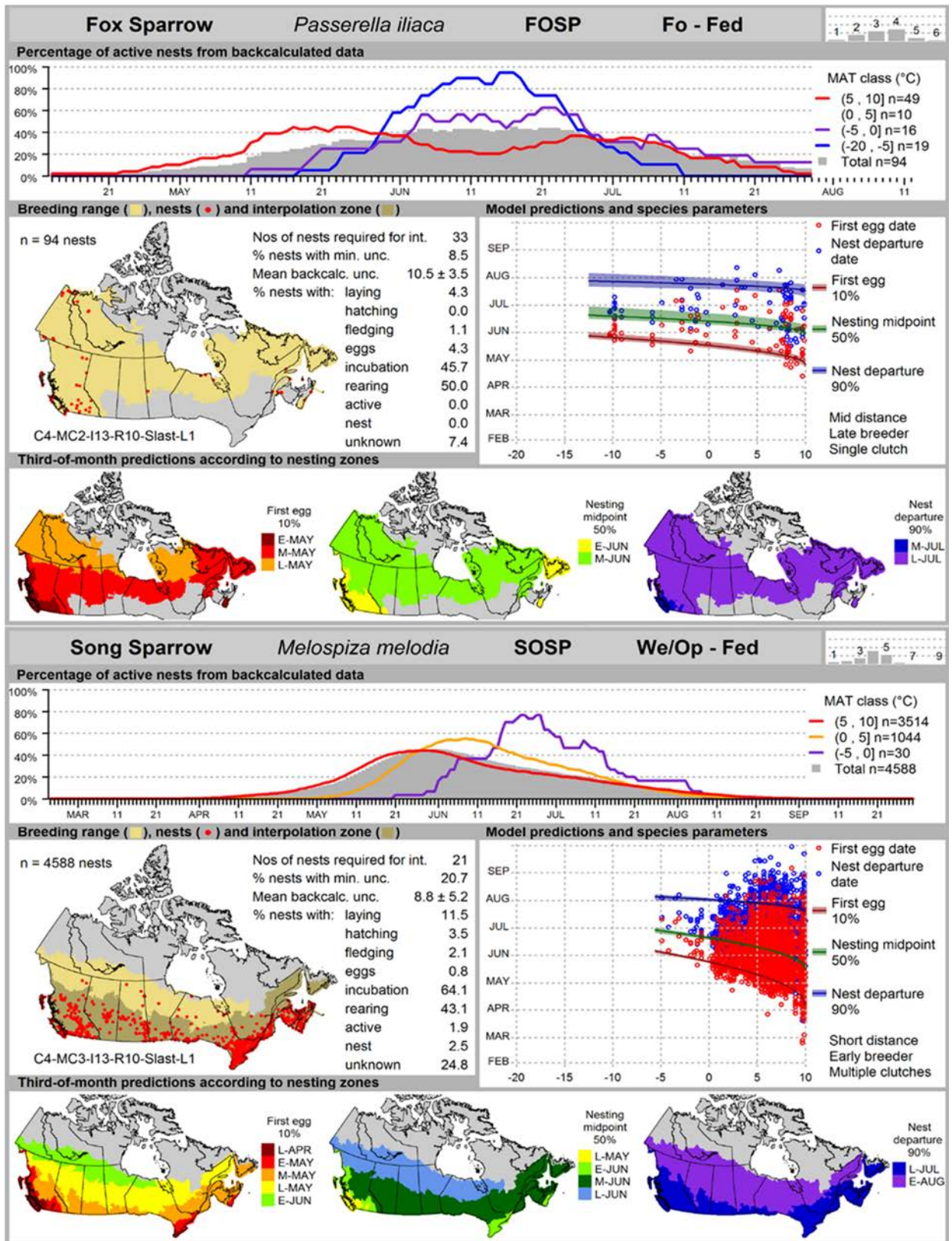


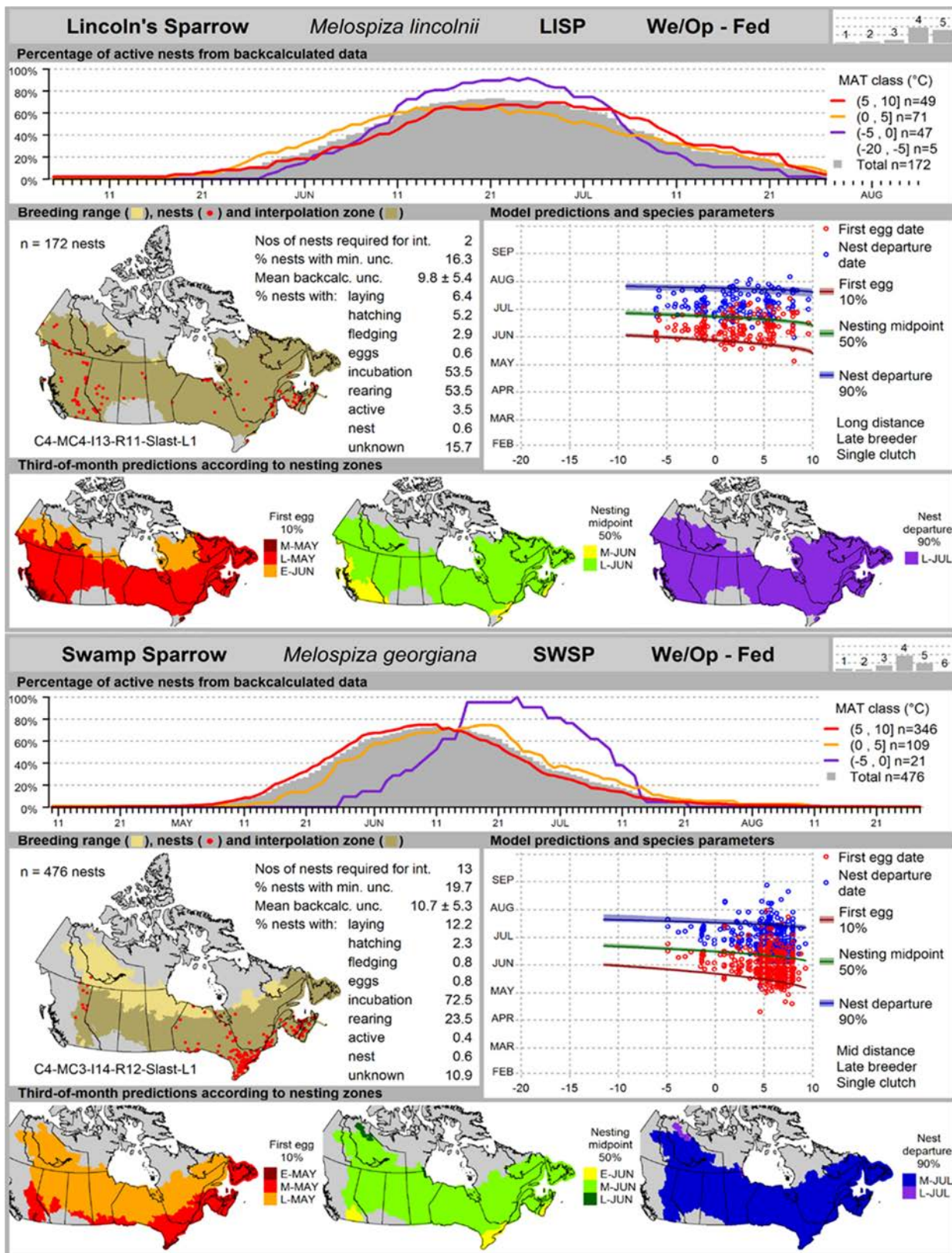


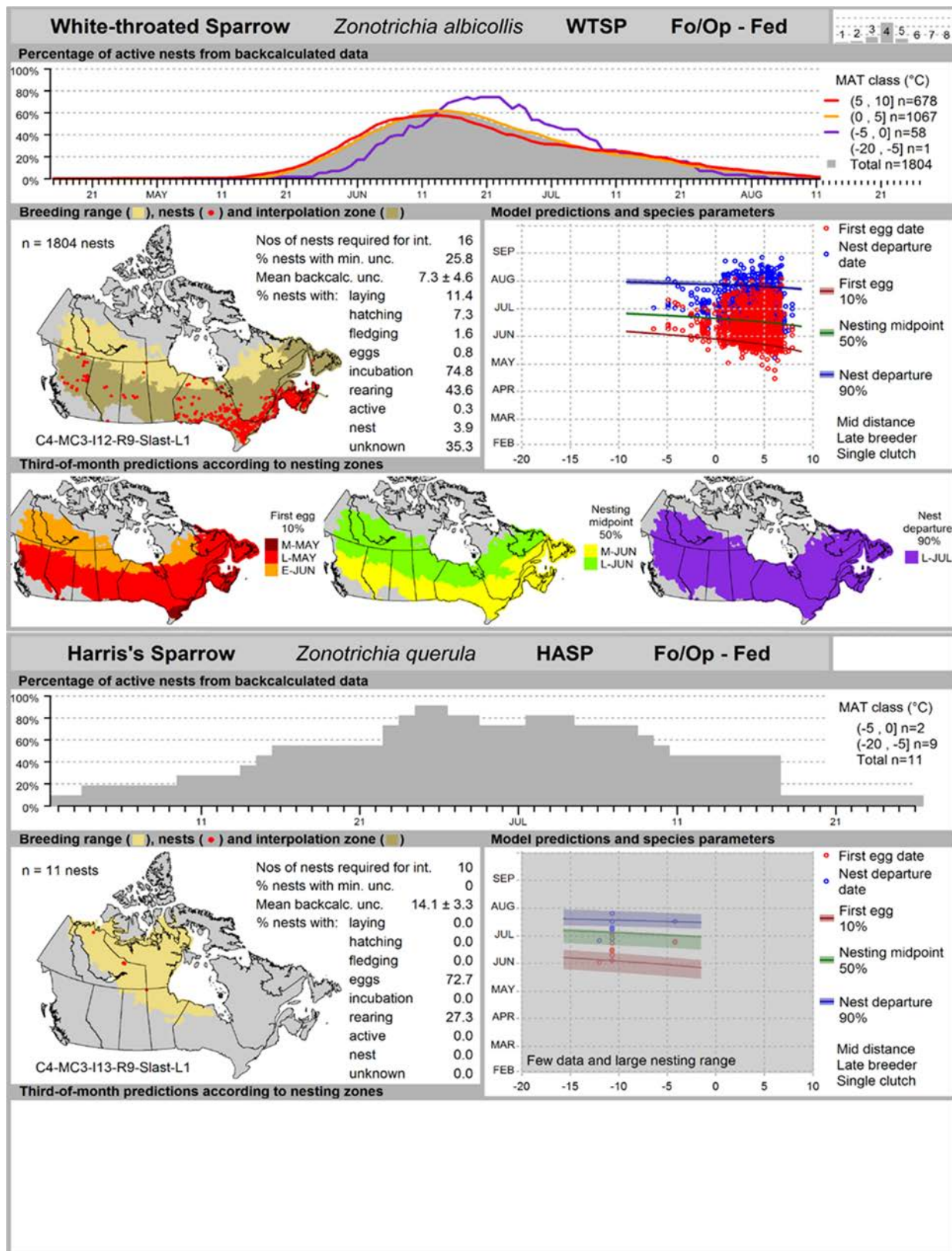


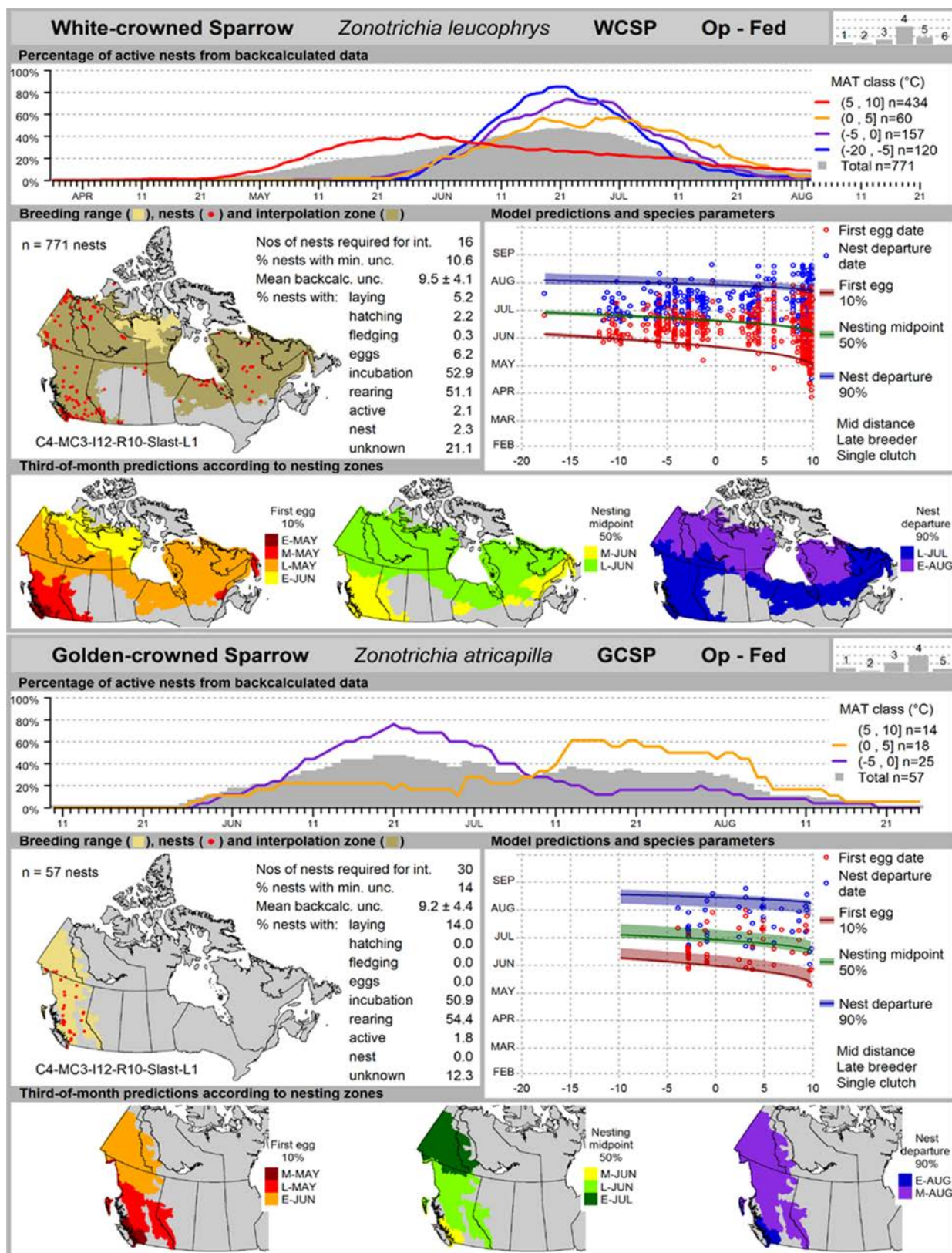


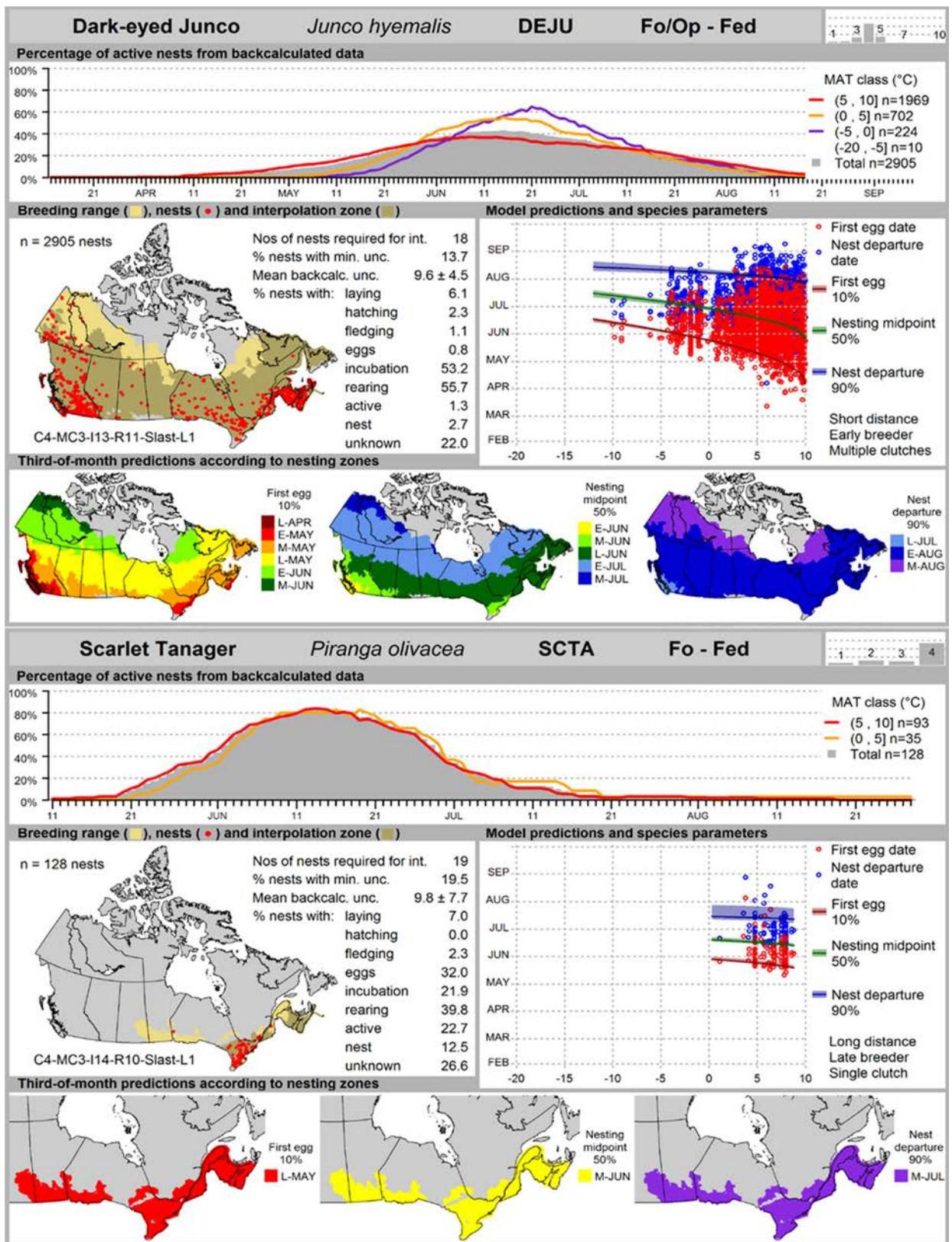


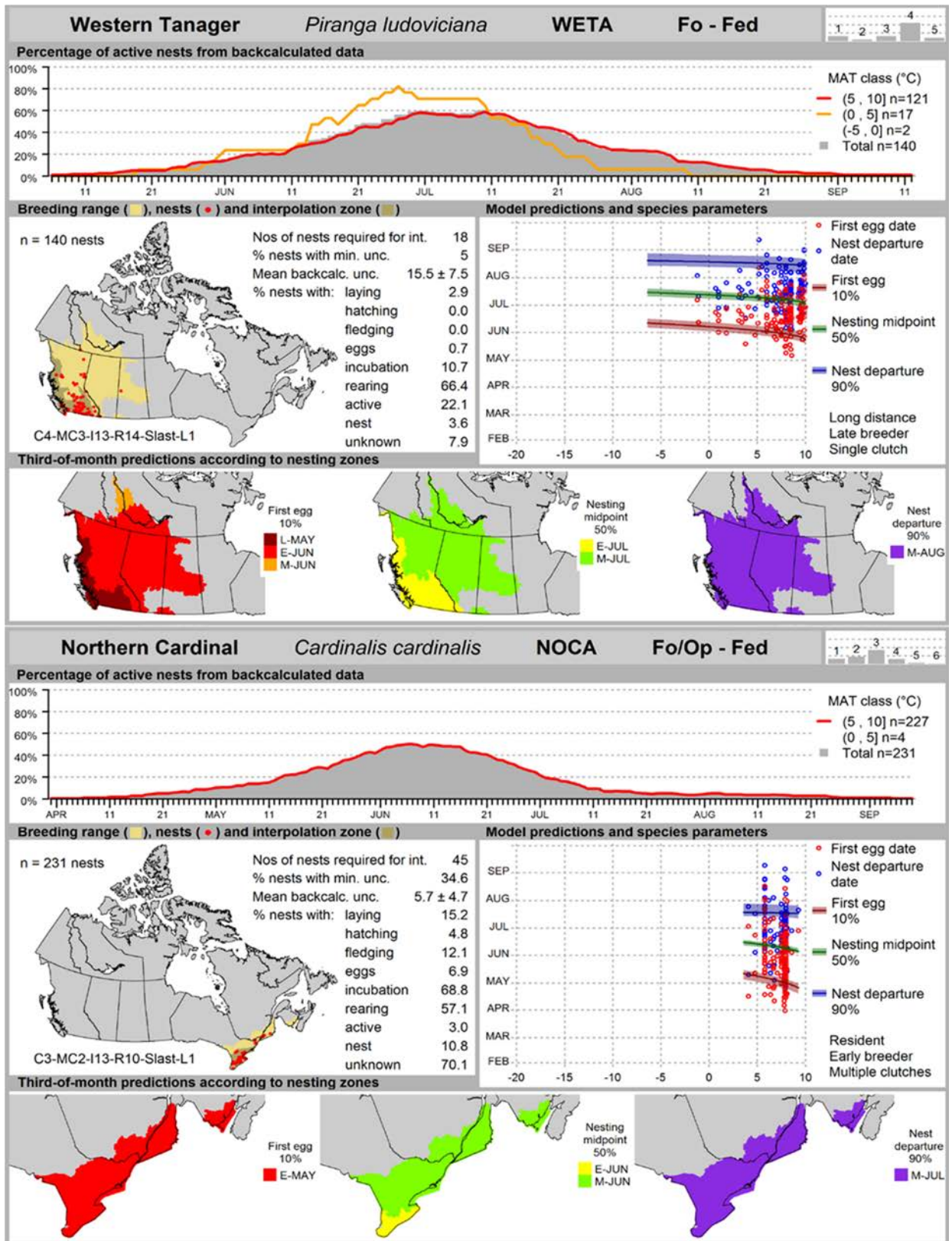


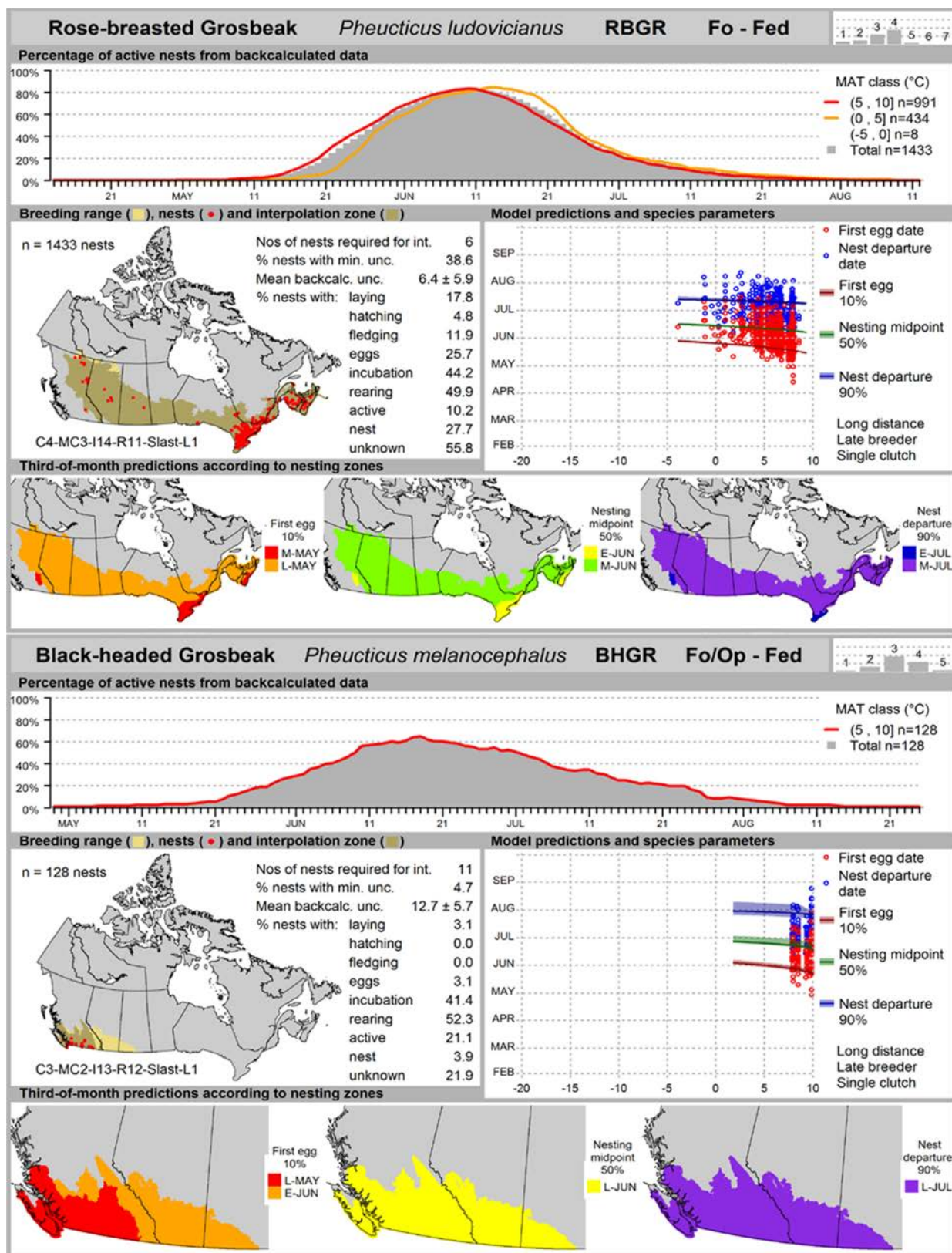


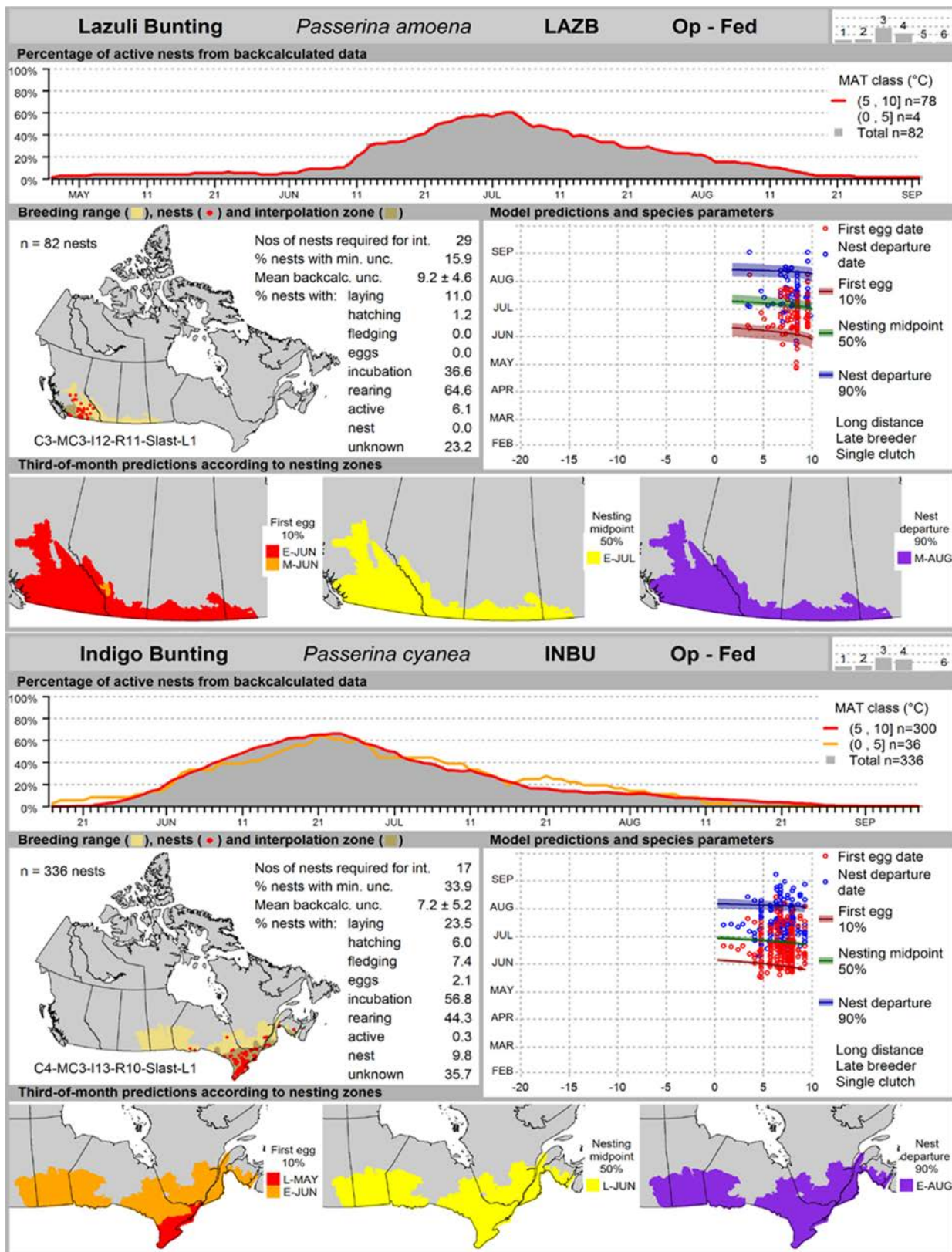


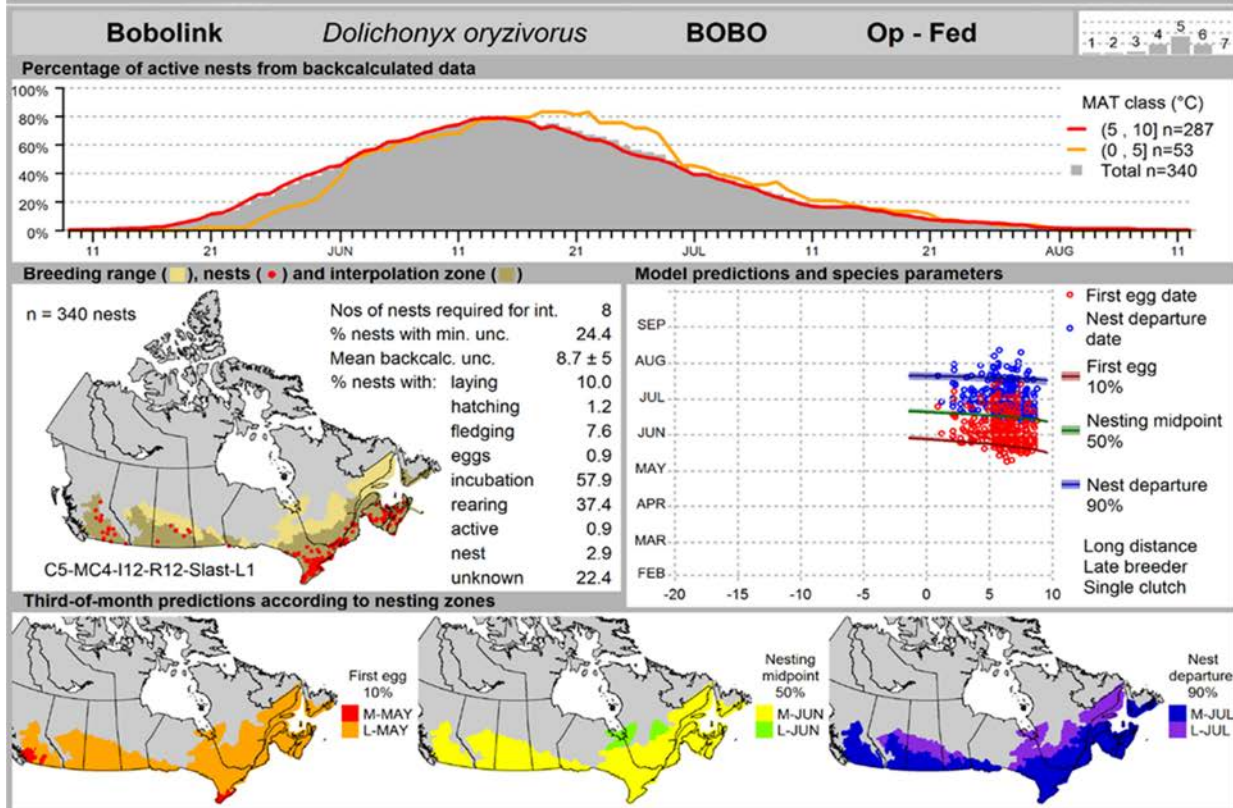
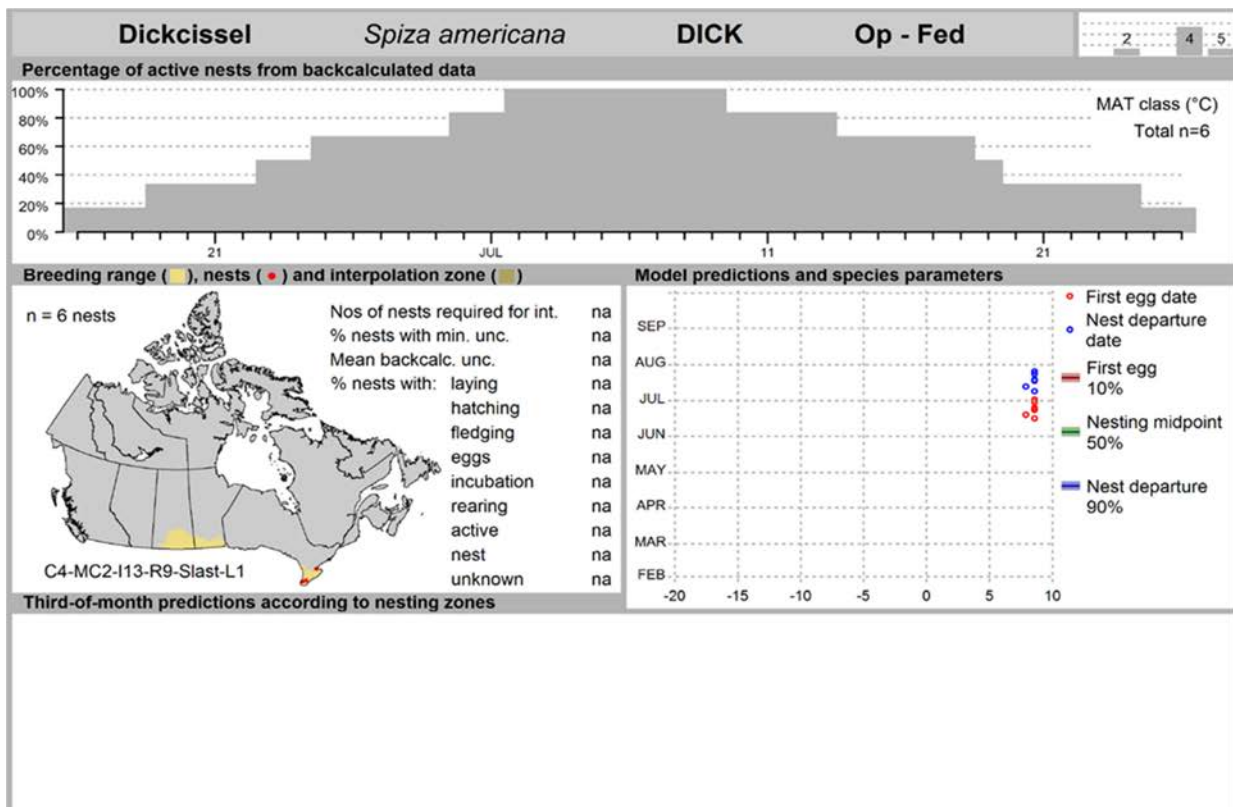


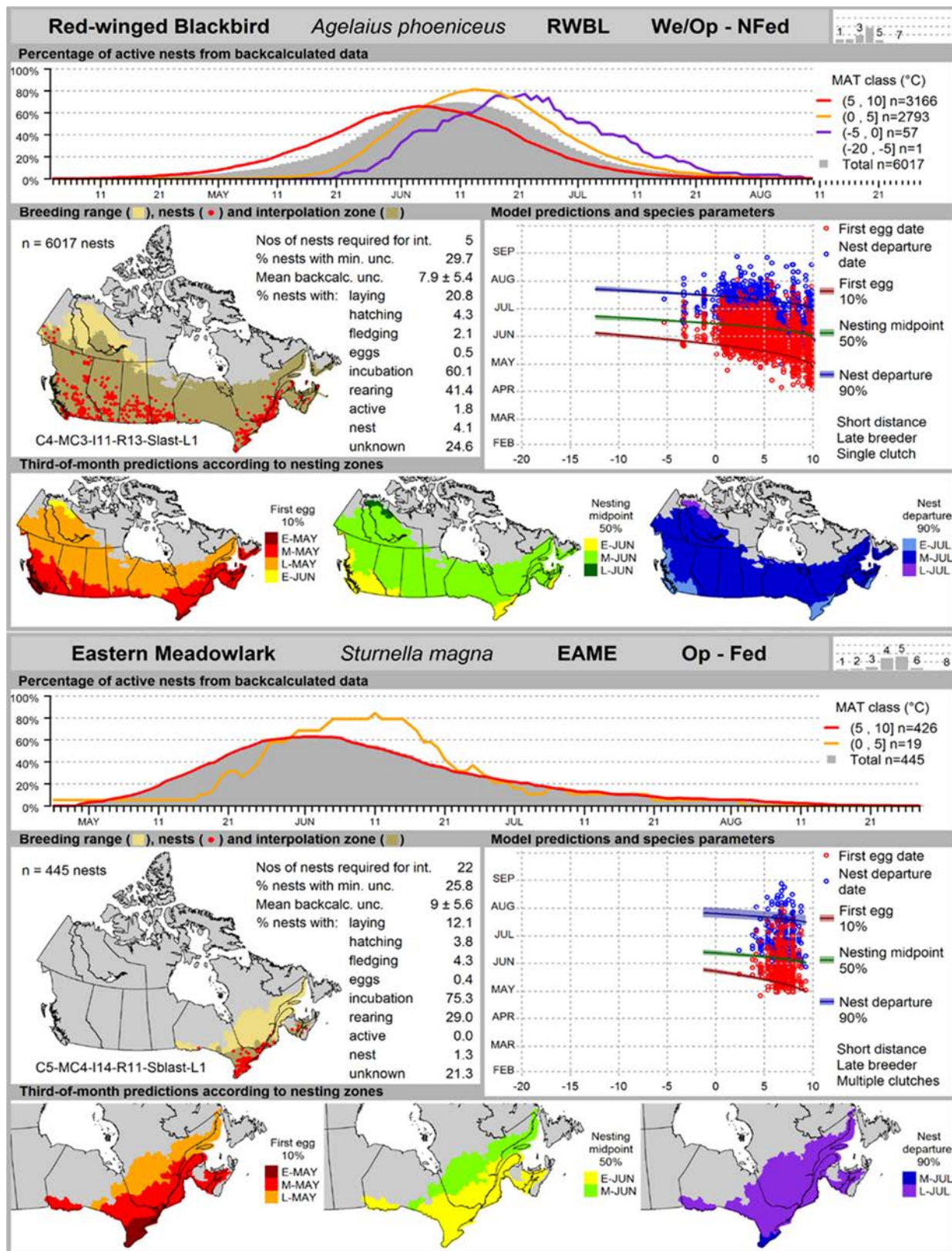


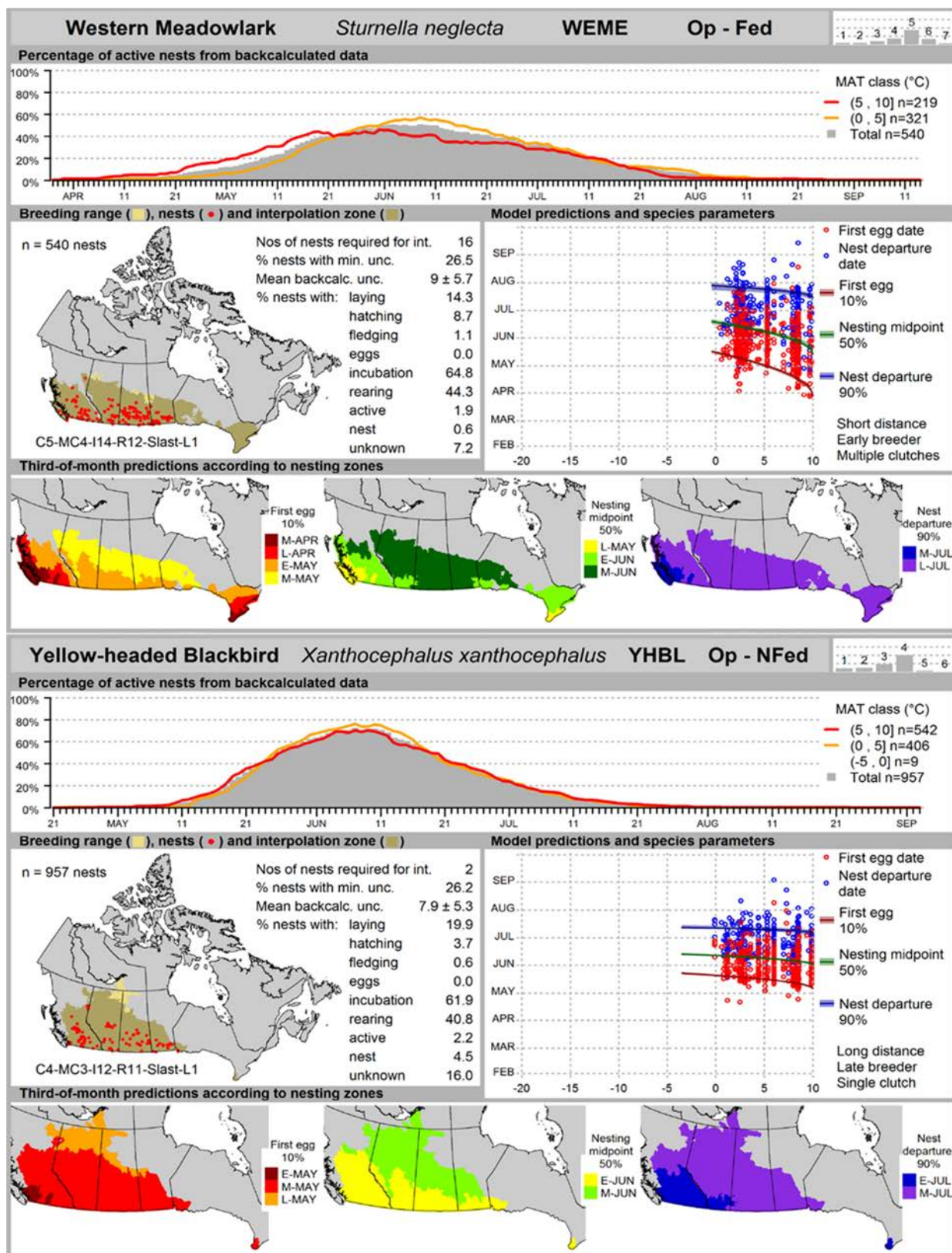


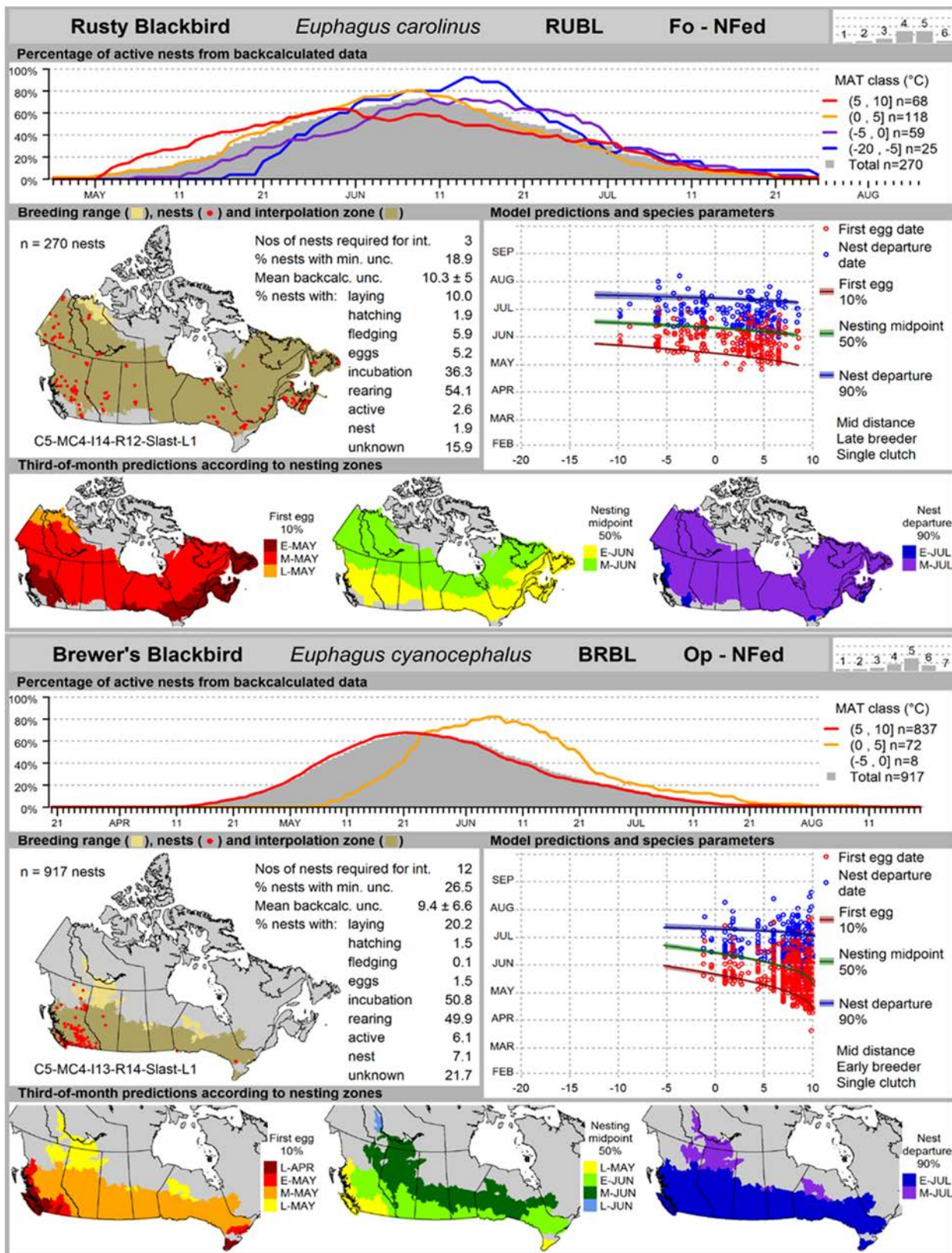


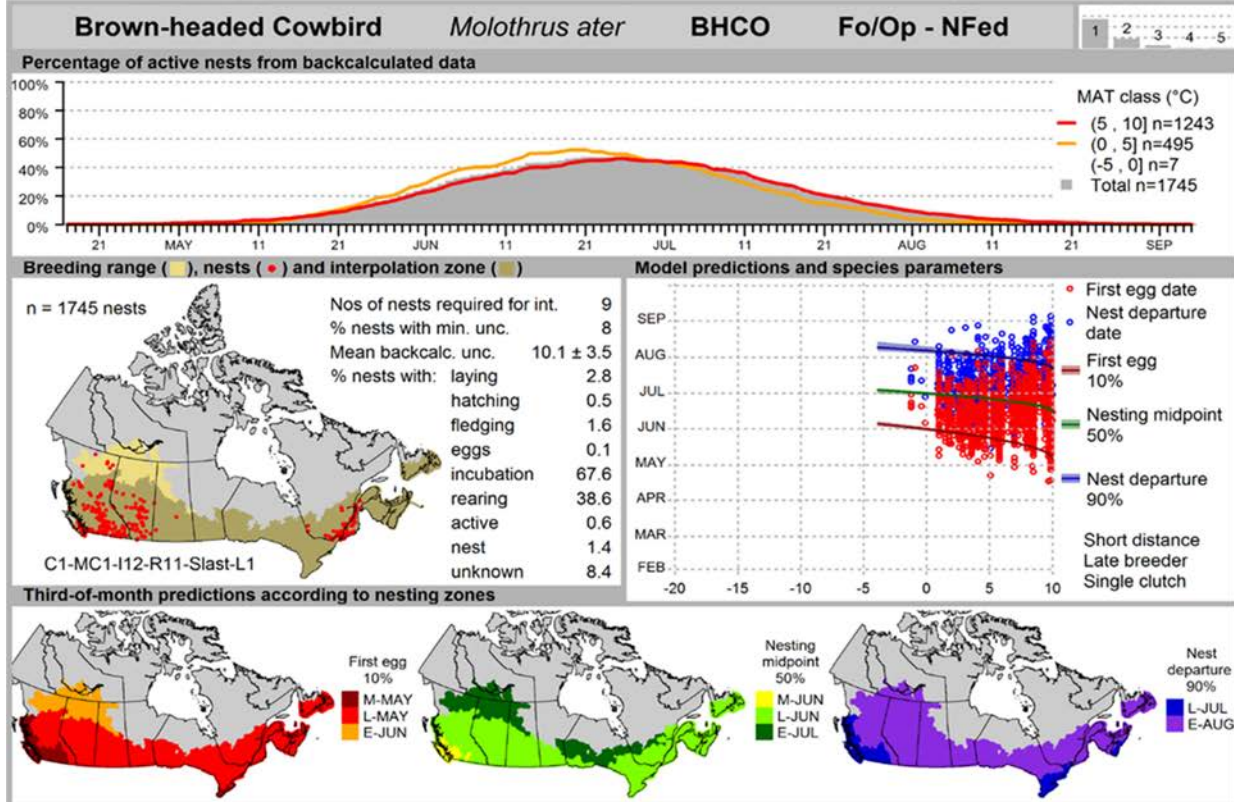
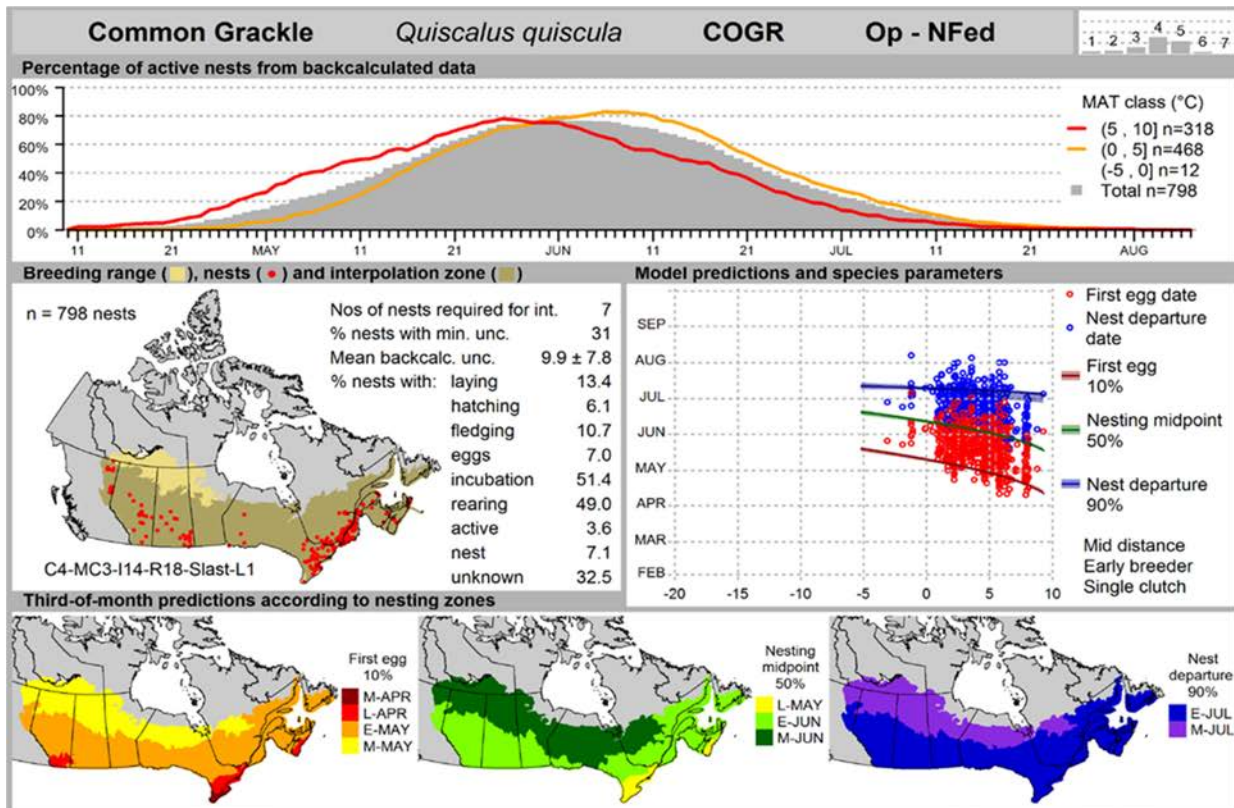


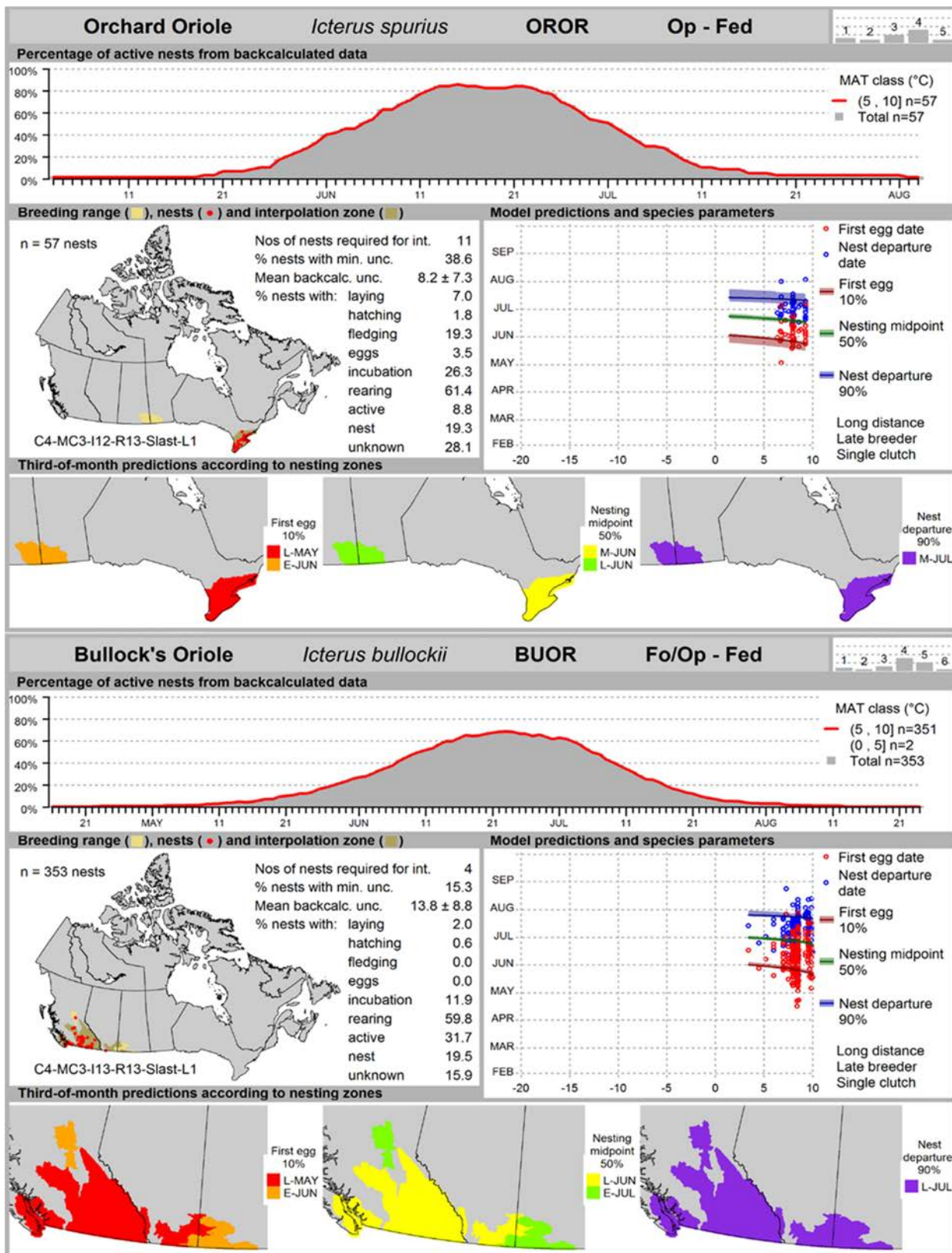


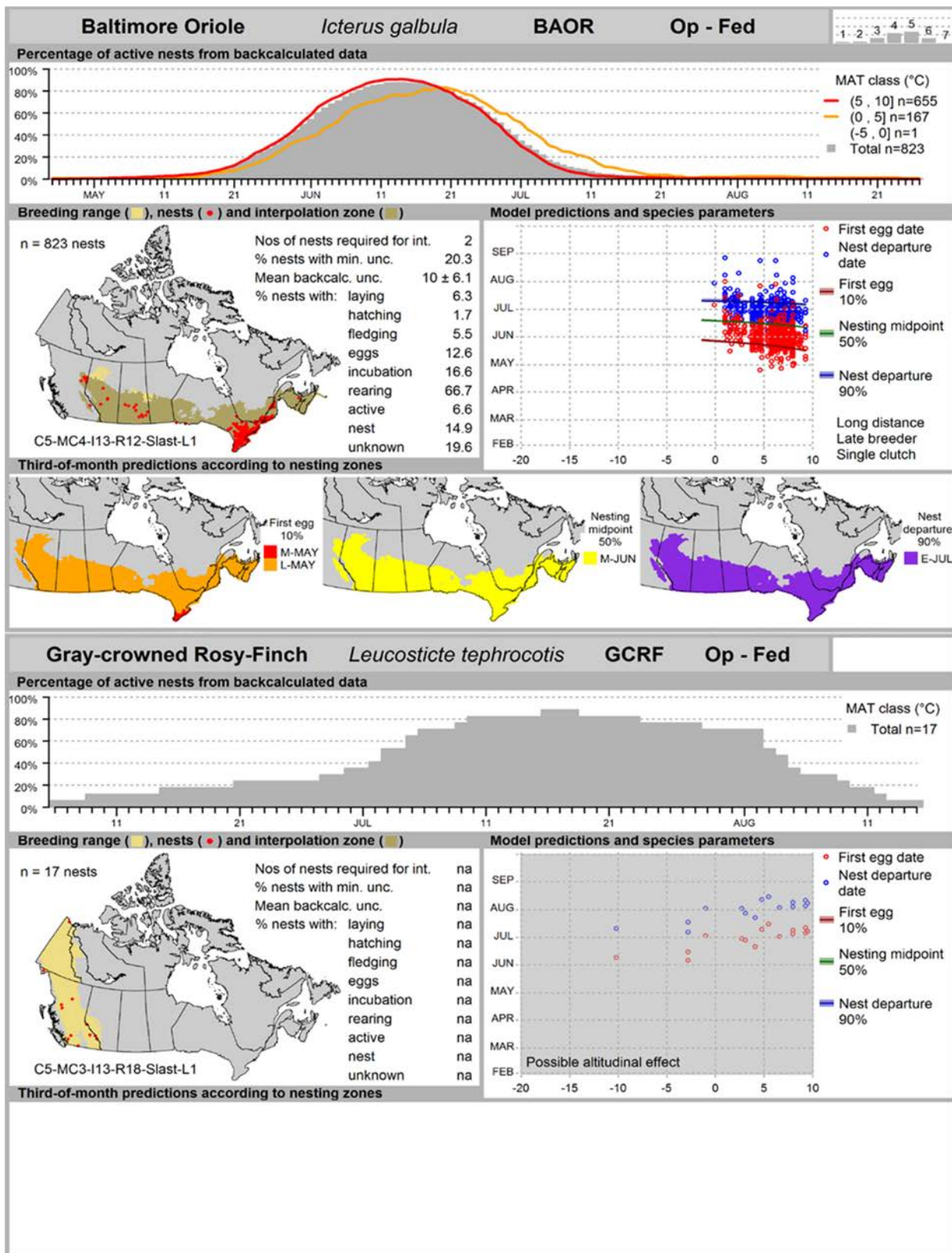


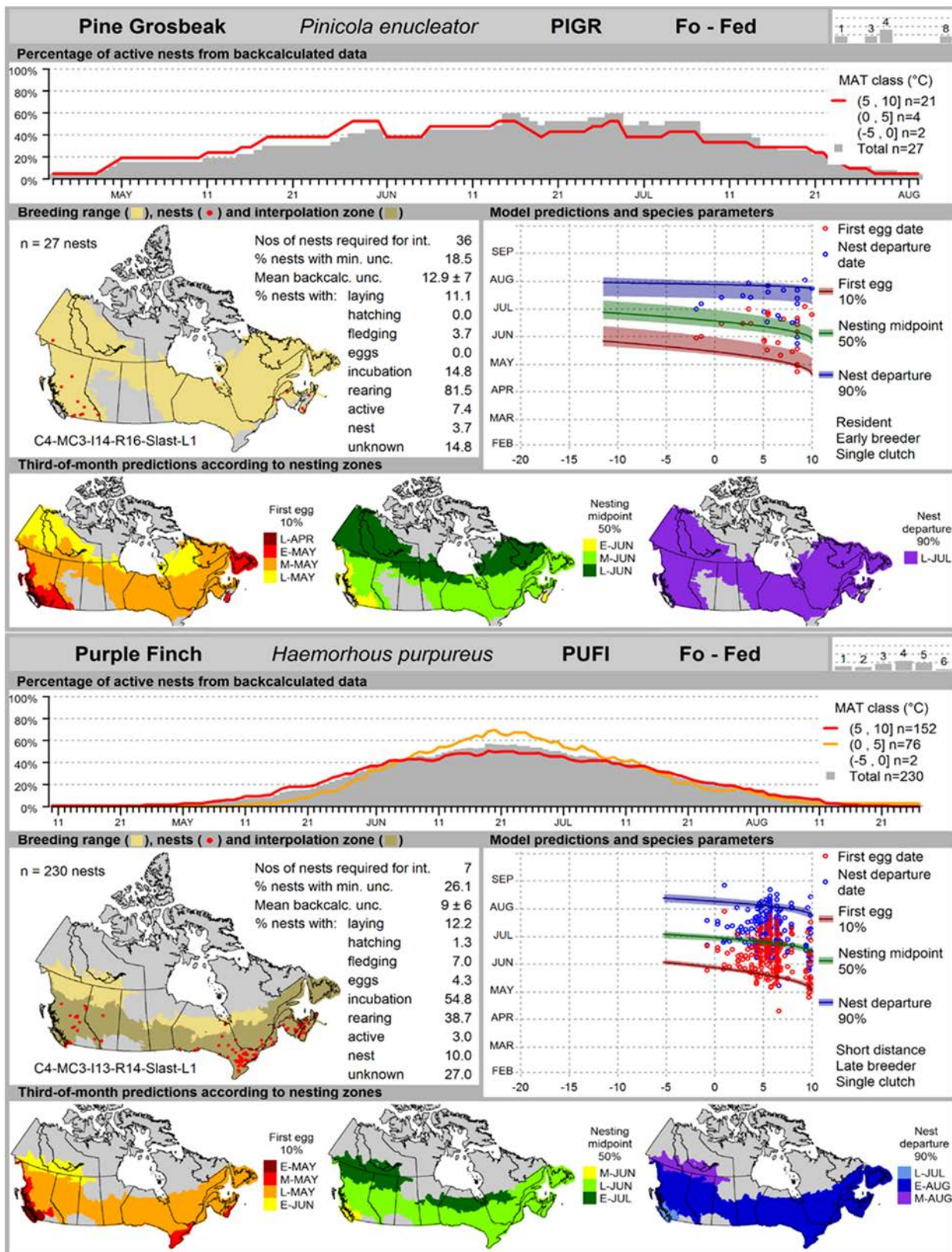


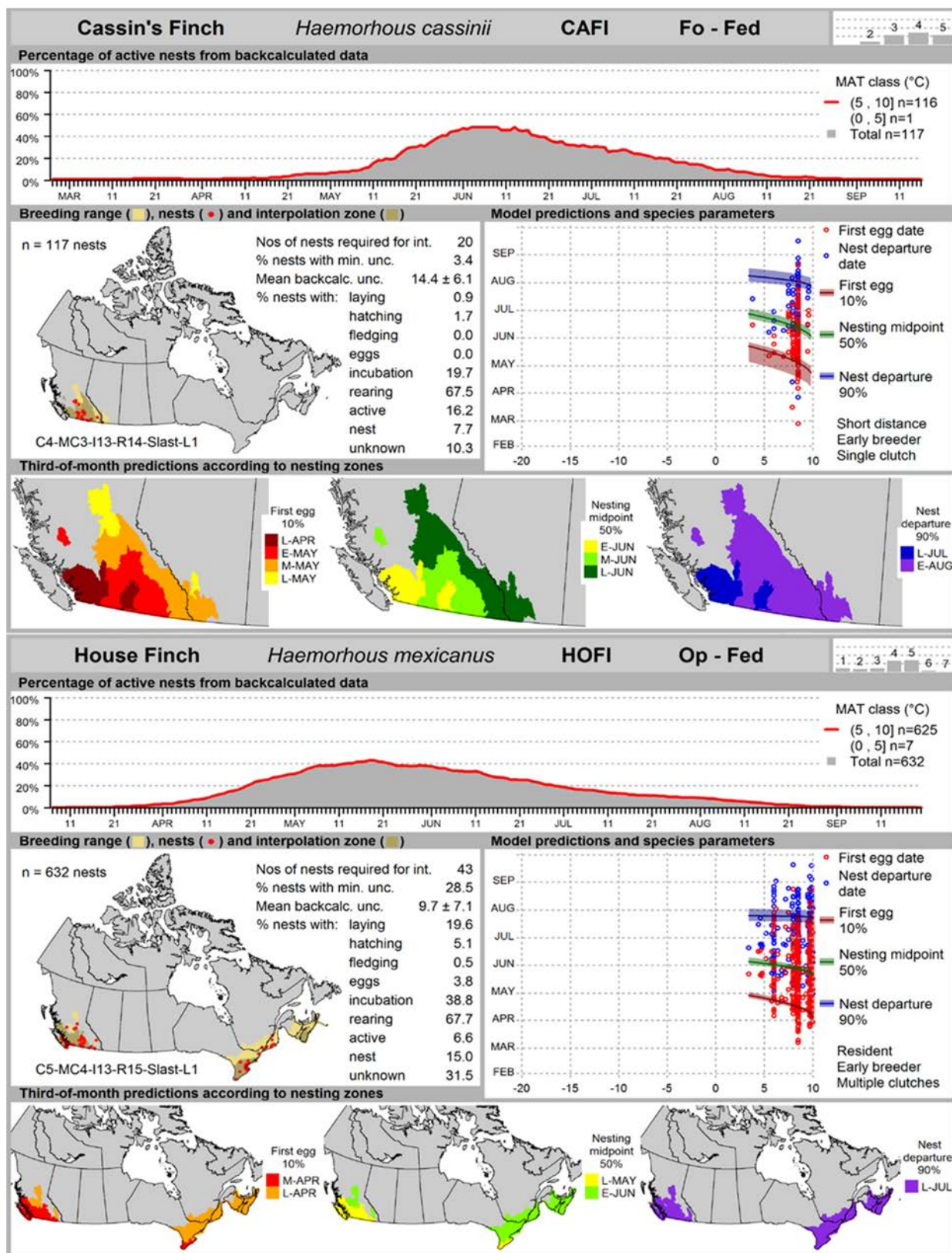


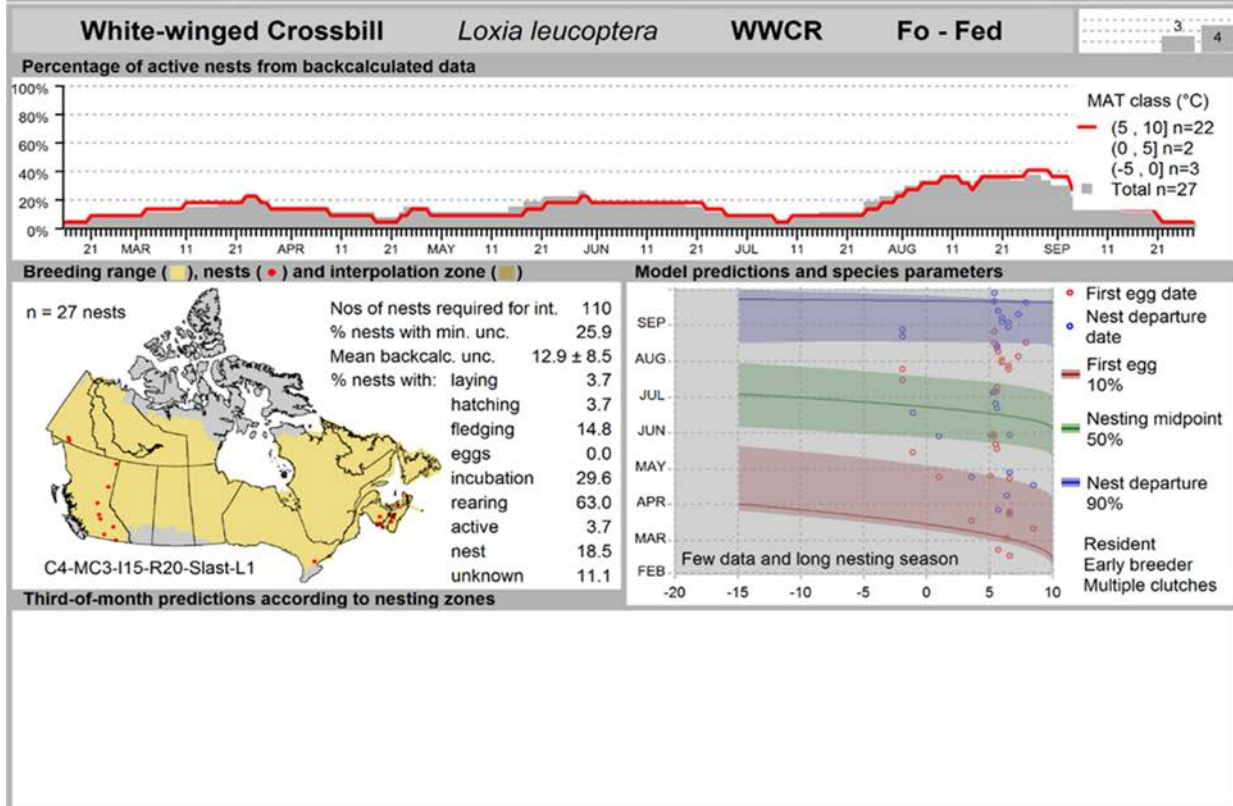
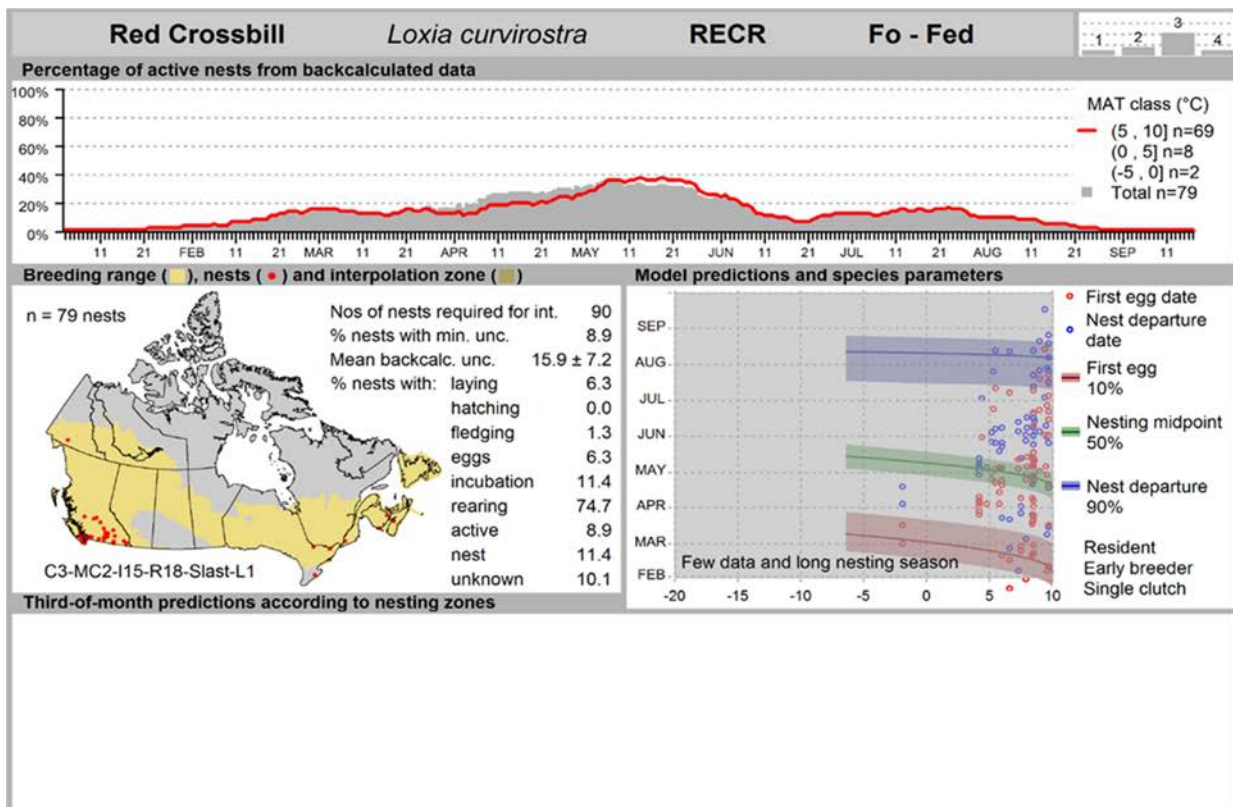


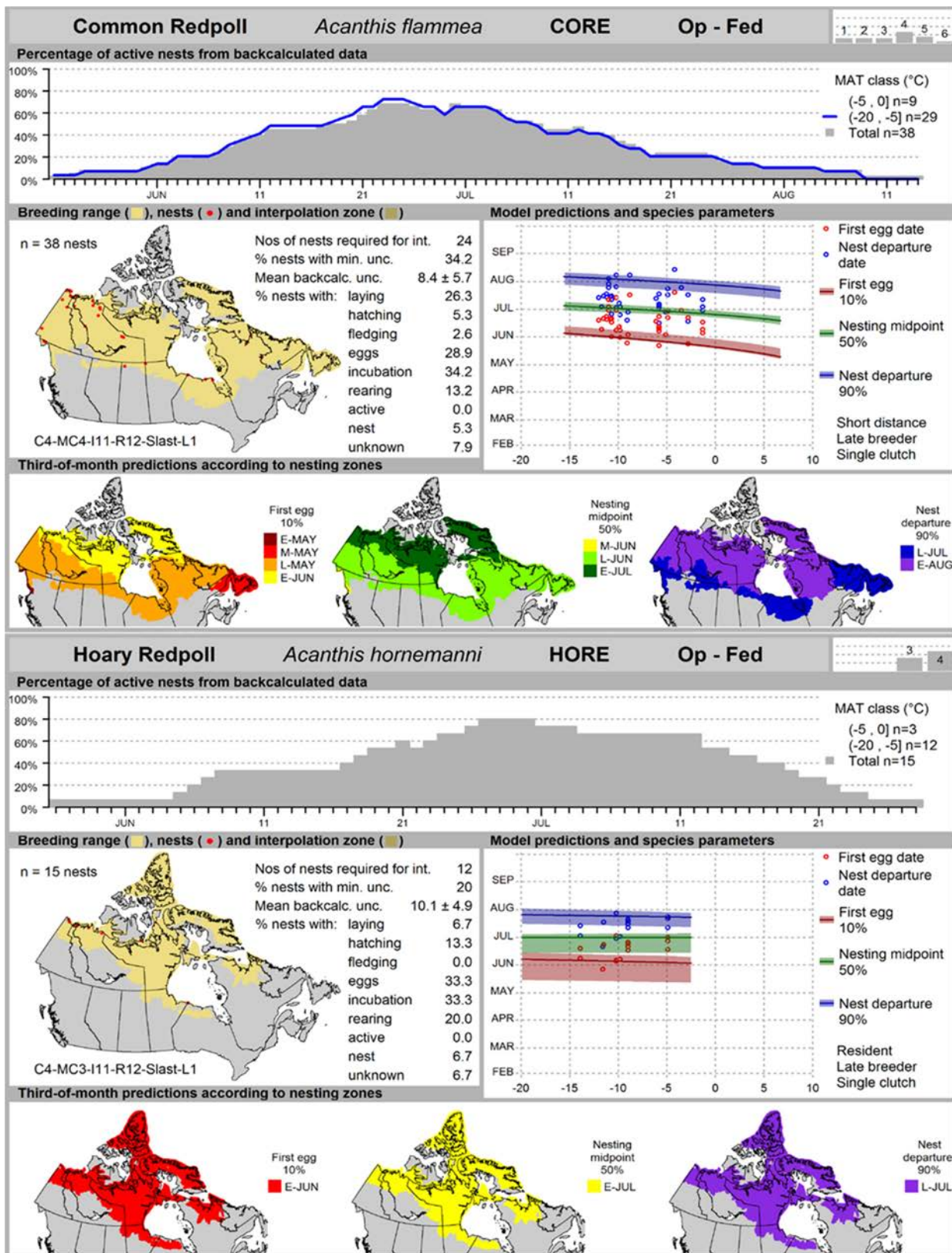


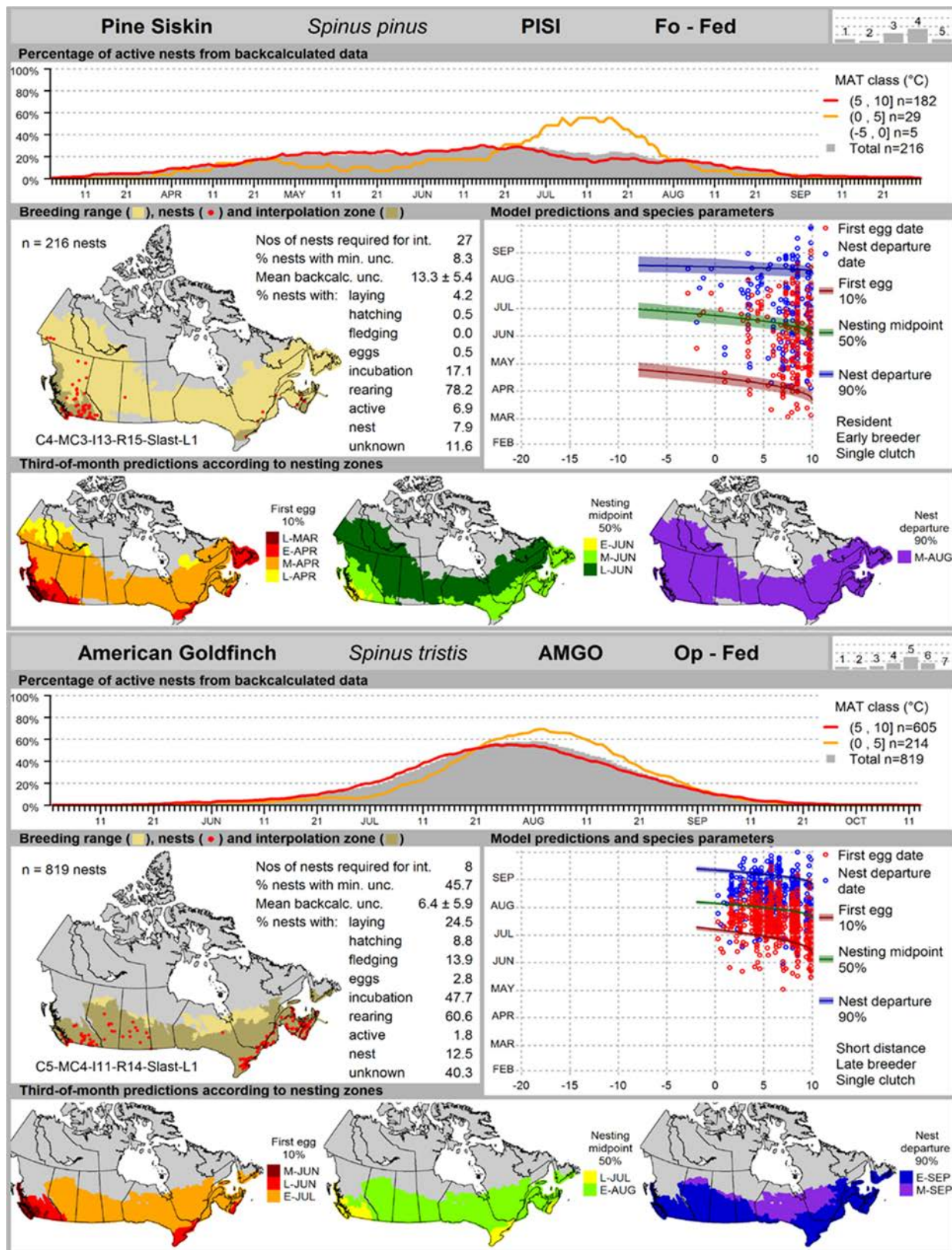


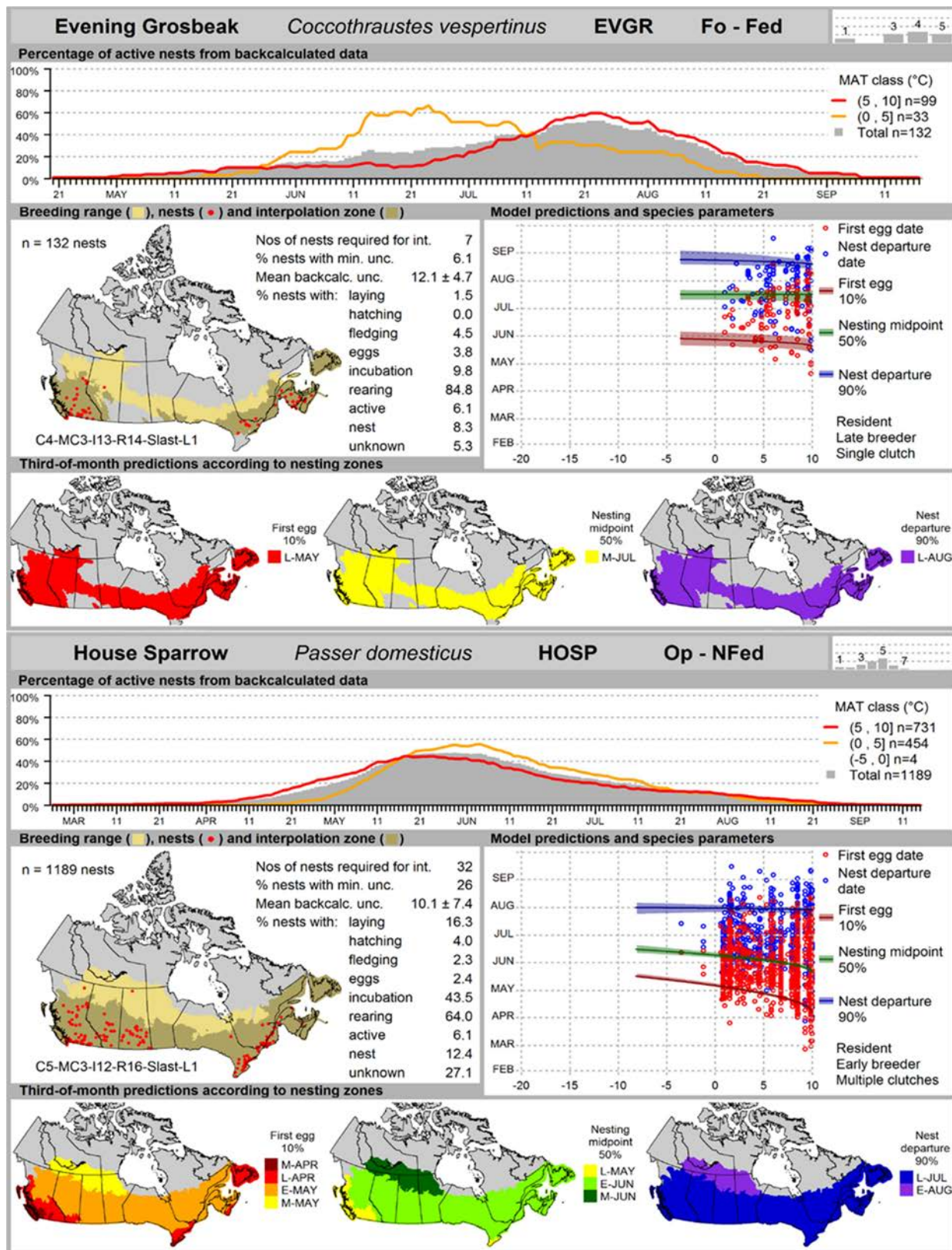












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(Photo: Herring or Great Black-backed Gull chick; B. Drolet)

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