Estimating rates of local extinction and colonization in colonial species and an extension to the metapopulation and community levels

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Coloniality has mainly been studied from an evolutionary perspective, but relatively few studies have developed methods for modelling colony dynamics. Changes in number of colonies over time provide a useful tool for predicting and evaluating the responses of colonial species to management and to environmental disturbance. Probabilistic Markov process models have been recently used to estimate colony site dynamics using presence–absence data when all colonies are detected in sampling efforts. Here, we define and develop two general approaches for the modelling and analysis of colony dynamics for sampling situations in which all colonies are, and are not, detected. For both approaches, we develop a general probabilistic model for the data and then constrain model parameters based on various hypotheses about colony dynamics. We use Akaike's Information Criterion (AIC) to assess the adequacy of the constrained models. The models are parameterised with conditional probabilities of local colony site extinction and colonization. Presence–absence data arising from Pollock's robust capture–recapture design provide the basis for obtaining unbiased estimates of extinction, colonization, and detection probabilities when not all colonies are detected. This second approach should be particularly useful in situations where detection probabilities are heterogeneous among colony sites. The general methodology is illustrated using presence–absence data on two species of herons. Estimates of the extinction and colonization rates showed interspecific differences and strong temporal and spatial variations. We were also able to test specific predictions about colony dynamics based on ideas about habitat change and metapopulation dynamics. We recommend estimators based on probabilistic modelling for future work on colony dynamics. We also believe that this methodological framework has wide application to problems in animal ecology concerning metapopulation and community dynamics.

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Colonial breeding is a form of group living in which individuals breed within densely distributed nesting territories that contain no resources other than nesting sites (Perrins and Birkhead 1983). Several orders of invertebrates (Alcock 1997) and vertebrates (e.g. fish: de Fraipont et al. 1993; reptiles and mammals: Trillmich and Trillmich 1984) are colonial, although among vertebrates coloniality is more common in birds, where about one species in eight breeds in colonies (Lack 1968). Coloniality in animals has been intensively studied from an evolutionary perspective (e.g. insects: Hamilton 1964, Wilson 1971; fish: Gross and MacMil-

lan 1981; reptiles: Trillmich and Trillmich 1984; birds: Wittenberger and Hunt 1985, Siegel-Causey and Kharitonov 1990, Rolland et al. 1998; mammals: Packer et al. 1990), but fewer studies have investigated the temporal and spatial dynamics of colonial breeding.

There are several reasons to model and understand colony dynamics and to work at the colony level. Colonial species are defined as usually colonial, i.e. breeding generally occurs in colonies but solitary pairs sometimes exist, or as strictly colonial, i.e. breeding always occurs in colonies. For those strictly colonial species and to a lesser extent for usually colonial species, individuals by definition can only have access to breeding through the existence of colonies. Hence, for colonial species colony dynamics may be closely linked to some important components of population dynamics such as fecundity. Animal movement is increasingly recognized as an important component of population dynamics and is explicitly considered in studies of temporal variation in colony site locations. Moreover, studies only focusing at the individual level in colonial species may not always identify factors affecting some components of population dynamics at the colony level. Therefore, modelling colony dynamics using estimated quantities that are relevant to theory and management should provide valuable insights for the ecology and conservation of colonial species.

The underlying processes of colony dynamics are similar to those of metapopulation dynamics which document patterns of patch occupancy, extinction and recolonization of local populations (Levins 1970, Hanski and Gilpin 1991). Most studies that have focused on colony dynamics have examined temporal variations using a colony-site turnover index, which combines colony-site extinction, colonization and annual differences in numbers of colonies (Erwin et al. 1981, Hecnar and M'Closkey 1996, Deerenberg and Hafner 1999). Because colony-site turnover indices combine extinction and colonization probabilities into a single parameter, they do not permit specific tests of hypotheses about factors affecting those probabilities, such as relevant year-specific and environmental co-variates. Similarly, they do not permit tests of the hypothesis that colony-site dynamics reflect a first-order Markov process in which state of the colony site (occupied or unoccupied) at time i depends on state at time $i-1$. Turnover indices represent descriptive statistics that are not useful for developing models for predicting the effects of future habitat or environmental change on colonies of interest.

Few studies have developed tools that permit the estimation of quantities such as extinction and colonization rates of colony sites and that permit tests of hypotheses about factors affecting those rates. Erwin et al. (1998) estimated extinction and colonization probabilities at several colony sites of gull-billed terns (*Gelochelidon nilotica*) in coastal Virginia, USA, in

sampling situations where all colonies are identified and detected with probability 1. Their approach has proven to be useful for estimating and testing the effects of habitat type and colony size on those rates. Their sampling situation implies that when no active colony is detected at a particular colony-site and at a particular time, then no colony is present.

However, in some sampling situations and for some species, colony detection probabilities may be <1, and analyses that ignore this uncertainty can lead to invalid inferences about variation in extinction and colonization rates over time. For example, a colony situated in high and dense vegetation may not be detected during an aerial survey at time i, and non-detection will be interpreted as absence if detection probability is assumed to be 1. If the colony was seen at time $i-1$ and at time $i+1$, this capture history will be erroneously recorded as extinction followed by a recolonization whereas the colony was continuously present. At present, animal population ecology at the colony level and animal metapopulation ecology at the local population level have not seen development of statistical inference procedures that recognize and incorporate colony (local population) detection probability.

Here, we present a methodological framework for modelling colony dynamics from presence–absence data at particular sites as a function of local extinction and colonization probabilities in the two sampling situations where all and part of the colonies are detected. In the case where not all colonies are detected, these methods also permit the estimation of colony detection probabilities. We illustrate these methods with data from two field studies of colonial nesting herons at Tour du Valat Biological Station, Camargue, France. Our modelling of these two data sets is based on a priori hypotheses and permits inference about habitat type and change on colony site dynamics.

Modelling and estimators of colony dynamics

The estimation approach that we will consider requires sampling an area (a group of potential colony sites) for colonies of one or more species for more than one time unit. We are interested in estimating quantities associated with changes in numbers of occupied colony sites during the intervals between sampling periods. Our estimators require estimates of the number and status (i.e. whether breeding individuals were seen or not) of colony sites within the surveyed area for each time period. We assume that all colony sites are identifiable and are geographically referenced. We are primarily interested in estimating extinction probability, which is defined as the probability that a site that has breeding individuals in year i has no breeding individuals in year $i+1$, and colonization probability, which is defined as

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the probability that a site that has no breeding individuals in year i has breeding individuals in year $i+1$. This estimation requires consideration of colony detection probability (p_i), which we defined as the probability of seeing breeding individuals at a colony site in year i, given that those individuals are present at the colony site in year i. We develop an initial approach for use when colony detection probability is equal to 1 but, as we suspect that colony detection probabilities are likely to be < 1 in some situations, we develop another approach for use when some colonies are likely to be missed during surveys.

Most studies that monitor colonies aim to estimate individual colony sizes and the population size of a given species for management and/or research purposes (see Thompson et al. 1998: 274–275). Such studies collect information about colony size and consequently about the presence–absence history of a colony at a given site. Colony censuses and surveys are conducted from the air, ground or water and are based primarily on visual cues. The result of a colony census or survey is a colony site list that identifies the sites where colonies were, and were not, detected. Thus, the data consist of the presence or absence of colonies at specific locations.

All colonies are detected

When all colonies are detected the detection probability equals 1, and we rely on the approach of Erwin et al. (1998) to estimate extinction and colonization probabilities. The data resulting from the study are summarized in colony site occupation histories (one for each colony site), which are rows of numbers conveying information about colony site status. When detection probabilities are 1, the sampling design requires only a single visit to each colony site at each sampling occasion, similar to the situation encountered in modelling capture–recapture data for "open" populations (Lebreton et al. 1992). A "0" denotes absence of breeding individuals during a sample period, and a "1" indicates that breeding individuals were present. For example, consider the following capture history for a four period study: 1011. This history reflects a site that had breeding individuals only in periods 1, 3, and 4. The colony site histories are analogous to the individual capture histories used in capture–recapture studies (Lebreton et al. 1992) and to the species presence/absence data used in community-dynamic studies (Nichols et al. 1998).

Using the notation of Erwin et al. (1998) we define the model parameters (Table 1). We then condition our analysis on the set of potential colony sites and treat the number of sites following the different possible patterns of colony site occupation as conditional multinomial random variables. We can then calculate the probability of the various possible colony site occupation histories. For example, the probability associated with the above history (1011) would be written as $(1 - \phi_1)\,\gamma_2\phi_3$. This probability is conditional on the initial state of the site, so the first "1" in the history is not modelled. Unlike the usual capture–recapture case in which we condition on the number of capture histories with at least one capture (at least a single "1" in the history), colony site occupation histories of all 0's are observable and are included in the probability model as well. The probability model for the entire data set is given by the product of these probabilities over all

Table 1. Parameters used in the modelling of colony dynamics and their description. p is the colony detection probability.

p	Parameters	Description of parameters
$p = 1$ (Erwin et al. 1998 approach)		
	ϕ_i	Probability that a site with breeding individuals at time i has breeding individuals at time $i+1$ ($1-\phi_i$ is a local extinction probability)
	γ_i	Probability that a site with no breeding individuals at time i has breeding individuals at time $i+1$ (γ_i is a colonization probability)
$p = 1$ (Multistate approach)		
	p_i^s	Probability of detection at time i for a colony site in state s ($s = 1, 2$)
	S_i^r	Probability that a colony site in state r ($r = 1, 2$) at time i survives until period $i+1$
	ψ_i^{rs}	Probability that a colony site in state r at time i, is in state s at time $i+1$, given that the colony site survived until $i+1$
	N_i	Total number of colony sites surveyed at time i
$p < 1$ (Robust design approach)		
	p_{ij}	Probability that breeding individuals are detected at a colony site in secondary sample j of primary period i, given that such individuals are present at the colony site during period i
	p_i^*	Probability that breeding individuals are detected at a colony site in at least one of the l_i secondary samples of the primary period i ($p_i^* = 1 - \Pi_{j=1}^{l_i}(1-p_{ij})$), given that such individuals are present
	ϕ_i^*	Probability that a colony site at time i survives until period $i+1$
	γ_i'	Probability that breeding individuals are not present during primary period i at a colony site, given that breeding individuals were not present in period $i-1$
	γ_i''	Probability that breeding individuals are not present during primary period i at a colony site, given that breeding individuals were present in period $i-1$
	N_i	Total number of colony sites surveyed at time i

colony site occupation histories, under the assumption of independence of fates and identity of rates among colony-sites. If covariates such as habitat type are hypothesized to be relevant, then models can be developed in which local extinction and colonization probabilities are functions of such variables. In the case where colony site dynamics reflect a first-order Markov process, ϕ_i and γ_i, are modelled separately, as described above, whereas in a non-Markovian model the probability that a site is occupied at time $i+1$ is given by a single parameter ($\phi_i = \gamma_i$) regardless of the previous history of the site.

Erwin et al. (1998) developed models of colony dynamics and implemented them in program SURVIV (White 1983). Here we implement the same kinds of models in program MARK (White and Burnham 1999), as we believe that this implementation will facilitate development and use of these models. This implementation in MARK requires that we translate the standard notation of MARK into that of Erwin et al. (1998), but we believe that this approach will ultimately benefit potential users. In order to implement these models in MARK, we rely on the multistate modelling approach of Brownie et al. (1993; see also Arnason 1973, Hestbeck et al. 1991, Nichols et al. 1992, 1993, Schwarz et al. 1993). In our case we can define a colony site state variable with two states: no breeding individuals present ("1") and breeding individuals present ("2"). Colony site occupation histories can be recoded using these two states. For example, occupation history 1011 would be recoded for use with MARK as 2122.

Model parameters for a multistate modelling approach (following model notation in Nichols et al. 1994) are then defined in the context of colony dynamics (Table 1). For the models discussed in this section, all colonies are detected, so $p_i^1 = p_i^2 = 1$. The survival probabilities, S_i^r, correspond not to colony occupancy, but to the colony site itself. In the usual case, colony sites are permanent ($S_i^1 = S_i^2 = 1$). If sites are lost through some sort of habitat destruction that renders them as no longer potential sites, then these survival parameters would be < 1. If colony sites can be lost, then the occupation history data would include a "0" in the first sampling period following the loss and in all subsequent periods.

The local extinction and colonization probabilities of our original model (see Erwin et al. 1998) are expressed in terms of the state transition probabilities of the MARK multistate parameterisation. Specifically, transition probability ψ_i^{21} denotes the probability that a site with breeding individuals in year i is found without breeding individuals in year $i+1$; hence $\phi_i = (1 - \psi_i^{21})$. Similarly, ψ_i^{12} denotes the probability that a site without breeding individuals in year i is found with breeding individuals in year $i+1$; hence $\gamma_i = \psi_i^{12}$. A constrained model with $\phi_i = \gamma_i$ (also written as: $(1 - \psi^{21}) = \psi^{12}$) would test for non-Markovian site dynam-

ics. Model fitting, estimation and testing can be carried out with program MARK and with program MSSUR-VIV (Brownie et al. 1993, Hines 1994).

All colonies are not detected

When the probability of detecting colonies is < 1, we rely on the robust design modelling approach of Pollock (1982, Kendall et al. 1997). Pollock's robust design involves sampling at two different time scales. Primary sampling periods are separated by times that are sufficiently large to expect changes in the population from one primary period to the next. In our numerical examples, we computed quantities relevant to change in colony site occupation occurring between primary sampling periods spaced 1 yr apart. Some number of secondary samples or sampling periods occurs within each primary period. The secondary samplings period should be sufficiently close together that we would not expect colony occupation status to change during the course of the secondary sampling. In our example, secondary samples are represented by two surveys made one month apart each year.

The colony site detection histories now have multiple entries corresponding to the secondary periods within each primary period. For example, consider the following detection history from a robust design study with 2 secondary periods in each primary period: 10 00 11. This detection history indicates that breeding individuals were detected at the colony site only during secondary period 1 of primary period 1 and during secondary periods 1 and 2 of primary period 3. In the usual capture–recapture framework, interior 0's for all secondary periods within a primary period (e.g. the 00 appearing during both secondary occasions of primary period 2 in the above history) indicate an individual that is present but not caught in the sampling period. However, in studies of colony dynamics, interior 0's in a colony site detection history can indicate either that breeding individuals were present but not detected, or that breeding individuals were not present (locally extinct), yet recolonized at a later time. In this respect, the modelling of colony site detection history data is similar to the modelling of species detection history data in community studies (Nichols et al. 1998), and is similar also to the modelling of capture–recapture data in the presence of temporary emigration. The robust design (Pollock 1982) provides the information needed to estimate quantities of interest in the presence of temporary emigration (Kendall et al. 1997), and also provides a basis for estimating colony dynamics parameters from detection history data.

For ease of implementation, we show how to implement them using the robust design routines in MARK. Using the model parameter notation similar to that of Otis et al. (1978), Seber (1982), and Kendall et al.

(1997), we can define the parameters used in the modelling of temporary emigration (Table 1). Under this parameterisation, ϕ_i^* denotes the survival probability of the site itself. In most sampling situations, colony sites are permanent and $\phi_i^* = 1$, although when this is not the case, loss of sites can be modelled. Relating the temporary emigration model parameterisation of Kendall et al. (1997) to the colony-dynamic notation presented above (see also Erwin et al. 1998), local extinction probability is now $\phi_i = (1 - \gamma_i'')$ and colonization probability is now $\gamma_i = (1 - \gamma_i')$. The parameter p_i^* corresponds to the probability of detecting breeding individuals at colony sites. A constrained model with $\phi_i = \gamma_i$ (equivalent to $\gamma_i'' = \gamma_i'$) would test for non-Markovian site dynamics.

We can write the probabilities associated with the different detection histories in terms of model parameters and thus obtain the probability model for the entire data set. For example, the probability associated with colony site detection history 10 00 11 would be written using our original notation for colonization and extinction probabilities as:

$$p_{11}(1 - p_{12})[\phi_1(1 - p_2^*)\phi_2 + (1 - \phi_1)\gamma_2]p_{31}p_{32},$$

or, using the temporary emigration model notation, as:

$$p_{11}(1 - p_{12})[(1 - \gamma_2'')(1 - p_2^*)(1 - \gamma_3') + \gamma_2''(1 - \gamma_3')]p_{31}p_{32}.$$

As noted above, p_i^* denotes the probability of being detected on at least 1 secondary sampling period during primary period i, and can be written as: $p_i^* = 1 - (1 - p_{i1})(1 - p_{i2})$. Model fitting, estimation and testing can be carried out with program MARK and with program RDSURVIV (Kendall et al. 1997, Kendall and Hines 1999).

Examples

The grey heron *Ardea cinerea*

We illustrate our approach to modelling colony dynamics with presence–absence data when $p = 1$ using data collected as part of a monitoring program of a population of grey herons at Tour du Valat, Camargue, France.

Field methods, hypotheses and statistical analysis

The data come from a 21-yr survey carried out annually from 1979 to 1999 (Moser 1984, Kayser et al. 1994). Every spring (late March) the Camargue delta complex was surveyed by air using a single-engine monoplane in order to locate breeding colonies and count the number of nests within each colony either from direct counts or from vertical photographs. Each year surveys were conducted over one or two days depending on meteorological conditions. We considered a site to be occupied by a colony if it contained at least one nest. Grey herons are sedentary in the Camargue and build their nests either in trees (*Tamarix gallica*, *Populus* sp., *Pinus* sp.) or in reed beds of *Phragmites australis* (Blondel 1965, Thomas and Hafner 2000), and all the suitable breeding sites (i.e. reed beds and woods) were surveyed each year at altitudes of 100 to 300 m above ground. Each colony site was located on an IGN (Institut Géographique National) 1:25 000 scale map and identified by a number, by habitat type (reed bed or tree), and by median colony size computed over the entire study period. Detection probability of colonies was assumed to equal 1 for the following reasons: breeding grey herons on nests appear almost white from the air, they build large nests (ca 1 m in diameter), and surveys are carried out when vegetation growth has not started yet (i.e. nest visibility bias due to vegetation cover is insignificant).

Hence, our raw data consisted of a matrix of 0's (no breeding birds detected) and 1's (breeding birds detected), with each row corresponding to a colony site characterized by its median colony size and by its habitat type. The data can be accessed at http://www.mbr.pwrc.usgs.gov/pubanalysis. We used the modelling approach described above to test several a priori hypotheses about grey heron colony dynamics.

First, we investigated whether colony dynamics reflected a first-order Markov process. This can be viewed as investigating state-dependence of colony dynamics, as the non-Markovian model encodes the hypothesis that occupancy of a colony site at time i does not depend on occupancy state at $i - 1$. Our prediction was that the probability of occupancy in year i should be higher for sites that were occupied in year $i - 1$ than for sites that were not (i.e. we predicted that $\phi_i > \gamma_i$). In the absence of dramatic habitat change, this prediction should hold whenever there is any degree of fidelity or tendency to return to the breeding location used the previous year, a common feature of many bird populations (Greenwood and Harvey 1982).

We also investigated models that did and did not include year-specificity of extinction and colonization probabilities. These models were not based on directional, a priori predictions, and we simply expected some evidence of temporal variation in this apparently dynamic system.

We investigated models in which extinction and colonization rates differed by the 2 main habitat types, reed bed and tree. We expected local extinction probabilities to be lower for the tree habitat as these were more stable (some reed beds were harvested). As habitat was represented by 2 general types, its effects were investigated via some models in which parameters were habitat-specific and other models in which they were not (habitat was not relevant).

We also investigated the hypothesis that local extinction probability is a function of colony "size", where size is measured in the number of breeding pairs as indexed by the number of nests counted from the air. We expected local extinction probabilities to be lower for larger colonies (sites with more nesting birds). This prediction emerges from various hypotheses. For example, if fidelity is perfect (all surviving birds return to their previous breeding colony), smaller colonies are expected to become "extinct" more frequently than large colonies simply because of demographic stochasticity (MacArthur and Wilson 1967, Goodman 1987). In cases where probabilities of returning to the breeding colony of the previous year are < 1, fidelity is often a function of reproductive success the previous year, with successful birds exhibiting a higher probability of returning than unsuccessful birds (reviews by Greenwood and Harvey 1982, Johnson et al. 1992). In other situations, birds may exhibit active habitat selection each year, choosing sites each year that appear to be of high quality (Johnson and Grier 1988). Under either of these scenarios, if habitat conditions are reasonably predictable from year to year, then we would expect higher probabilities of returning to sites with larger breeding colonies. Any sort of social facilitation or attraction (Wilson 1975) combined with some degree of fidelity should also lead to lower probabilities of local extinction for larger colonies.

We thus included models in which annual extinction probability, ϕ_i, was modelled as a linear-logistic function of median colony size:

$$\text{logit}(\phi) = \log\left(\frac{\phi}{(1-\phi)}\right) = \alpha + \beta \times s,$$

where α and β are the intercept and slope parameters, respectively, and s is the median colony size.

Model fit was assessed using program SURVIV and model parameter estimation and testing were carried out using program MARK. Note that the 2 programs were used to implement the same models and thus produced nearly identical model selection statistics and parameter estimates. The most general model ($\phi_{h \times i}$, $\gamma_{h \times i}$) in the model set contained time-specific (i) parameters that differed between habitats (h) and assumed that colony site dynamics reflect a first-order Markov process. We then built reduced-parameter models by constraining extinction and colonization probabilities to be constant over time and/or habitat in order to test hypotheses about time and habitat effects. We used Akaike's Information Criterion for model selection (AIC, Akaike 1973, Burnham and Anderson 1992, 1998, Lebreton et al. 1992), selecting the model with the lowest AIC as the most appropriate one for use in estimation. As the most general model was saturated, there was no need for a quasi-likelihood adjustment of AIC values. Low-AIC models are parsimonious as they fit the data reasonably well with a relatively small number of parameters. Because our sample sizes were not large relative to the number of parameters in our general model, we used AICc, a modified criterion with small-sample bias adjustment (Burnham and Anderson 1998).

Results

Models with non-Markovian extinction and colonization had large ΔAICc values and did not fit the data whereas low AICc Markov process models fitted the data reasonably well (Table 2). When modelling the effects of time and habitat on extinction and colonization probabilities, the best model was (ϕ, γ_{h+i}), with associated model weight $w = 0.822$ as a strength of evidence for this best model. The evidence for a time effect on colonization is very strong in that the sum of the AICc weights for the first three models in Table 2 was 0.998. The additional hypothesized effect of habitat was supported by the data as one can see that ΔAICc for model (ϕ, γ_i) with number of parameters np $= 21$ increased by more that 3 units over model (ϕ, γ_{h+i}) with np $= 22$. However, the effect of habitat on extinction was not supported by the data since ΔAICc for model (ϕ_h, $\gamma_{h \times i}$) with np $= 42$ increased by nearly 2 units over model (ϕ, $\gamma_{h \times i}$) with np $= 41$. Under model (ϕ, γ_{h+i}), the estimated annual extinction probability was: $1 - \hat{\phi} = 0.27$ ($\hat{\text{SE}} = 0.02$). Colonization probabilities varied with time and habitat and tended to be higher in the reed bed habitat than in the tree habitat (Fig. 1a). Standard errors for the colonization probability estimates were relatively high for some years. Such poor precision will likely be common when time-specific parameters are needed with small to medium sized samples.

The model with median colony size as an individual covariate, model (ϕ_{Siz}, γ_{h+i}) where colonization was time and habitat-specific and extinction was colony size-specific, had a lower AICc value than previous models (Table 2). The ΔAICc between model (ϕ_{Siz}, γ_{h+i}) and model (ϕ, γ_{h+i}) was 29.2, indicating a strong effect of colony size on extinction probability as model (ϕ_{Siz}, γ_{h+i}) has $w = 1.0$. The slope parameter for the linear-logistic model was $\hat{\beta} = -0.644$ ($\hat{\text{SE}} = 0.140$), indicating that extinction probability decreased with increasing colony size (Fig. 1b).

The purple heron *A. purpurea*

To illustrate the approach for modelling colony dynamics when $p < 1$, we use data collected as part of a monitoring program of a population of purple herons at Tour du Valat.

Table 2. Goodness-of-fit statistics, AICc and ΔAICc (Δ) values, AICc weights (*w*) and number of parameters (np) for various models of colony site dynamics expressing different biological hypotheses about time and habitat variations in extinction and colonization probabilities of grey herons in southern France. Models are ranked according to Δ, which is defined as the difference between the AICc of a model and the AICc for the minimum AICc model. The likelihood of a model, given the data, was estimated with a likelihood-based inference approach with AICc weights (*w*) following Anderson et al. (2000).

Models	Goodness-of-fit			AICc	Δ	*w*	np	Biological hypothesis
	χ^2	df	*P*					
$(\phi_{Siz}, \gamma_{h+i})$	−†	–	–	1141.4	0	≅ 1	23	Colony size-specific extinction, and time and habitat-specific colonization without interaction
(ϕ, γ_{h+i})	70.5	57	0.11	1170.6	29.2	<0.001	22	Constant extinction, and time and habitat-specific colonization without interaction
(ϕ, γ_i)	69.1	58	0.15	1173.8	32.4	<0.001	21	Constant extinction and time-specific colonization
$(\phi, \gamma_{h \times i})$	39.1	38	0.42	1180.8	39.4	<0.001	41	Constant extinction and time and habitat-specific colonization
$(\phi_h, \gamma_{h \times i})$	39.3	37	0.37	1182.2	40.8	<0.001	42	Habitat-specific extinction, time and habitat-specific colonization
(ϕ, γ_h)	141.0	76	<0.001	1197.1	55.6	<0.001	3	Constant extinction and habitat-specific colonization
$(\phi_i = \gamma_i)$	527.0	60	<0.001	1204.8	63.4	<0.001	20	Time-specific site occupancy
$(\phi_{h \times i} = \gamma_{h \times i})$	489.9	40	<0.001	1211.1	69.7	<0.001	40	Habitat and time-specific site occupancy
$(\phi_{h \times i}, \gamma_{h \times i})$	0.0	2	1.0	1215.7	74.3	<0.001	78	Time and habitat-specific extinction and colonization
$(\phi_h = \gamma_h)$	539.7	75	<0.001	1222.7	81.3	<0.001	2	Habitat-specific site occupancy
$(\phi = \gamma)$	538.7	79	<0.001	1229.3	87.9	<0.001	1	Stochastic site occupancy

† No goodness-of-fit test is yet available for models with individual covariates.

Field methods, hypotheses and statistical analysis

Purple herons are trans-Saharan migratory birds that arrive on the breeding grounds in the Camargue in April. They build their nests exclusively in reed beds. Every spring (May) the Camargue delta complex was surveyed by air using a single-engine monoplane in order to locate breeding colonies and count the number of nests within each colony either from direct counts or from vertical photographs (Moser 1984, Kayser et al. 1994). Each year two surveys (early May and late May) were conducted. We considered a site to be occupied by a colony if it contained at least one nest. All the suitable breeding sites (i.e. reed beds) were surveyed each year from altitudes of 100 to 300 m above ground. Each colony site was located on an IGN 1:25 000 scale map and identified by a number, and by median colony size computed over the entire study period. The following reasoning led us to suspect that detection probability of colonies of purple herons were <1: breeding purple herons on nests are brownish and may not be easily distinguished in reed beds from the air, they build relatively small nests (ca 0.5 m in diameter), and surveys are carried out when vegetation growth has already started (i.e. nests may be invisible within reed beds as reed stems grow up to 2 m high). The data come from a 20-year survey carried out annually from 1981 to 2000.

For the purple heron our raw data consisted of a matrix of 0's (no breeding birds seen) and 1's (breeding birds seen), with 20 primary sampling periods (years) and 40 secondary sampling periods (early and late May), each row corresponding to a colony site characterized by its median colony size. Previous work on purple herons in the Camargue has provided evidence that colony site dynamics are affected by water levels and reed harvesting intensity (Barbraud and Mathevet 2000, Barbraud et al. in press). Consequently, we divided the study area in three regions based on differences in interannual water level stability and reed harvesting intensities (Mathevet 2000). The eastern region was slightly harvested (ca 2.5% of the total reed bed area was harvested) with stable water levels, the central region was intensively harvested (ca 18%) with very variable water levels, and the western region was intensively harvested (ca 17%) with stable water levels. These harvesting percentages represent the average amount of reed bed harvested per year.

Modelling for these data were directed at 2 different classes of questions. First, we were interested in developing a reasonable means of modelling detection probability. Specifically, we tested for temporal variation in detection probabilities associated with primary and secondary periods. We also tested for the possibility that within a primary sampling period, colony sites at which colonies were detected in the first secondary sampling period might have different detection probabilities in the second secondary sampling period than occupied sites at which colony presence had not been detected previously. This model was considered because both flights were sometimes conducted by the same observer who might have recalled detections from the previous
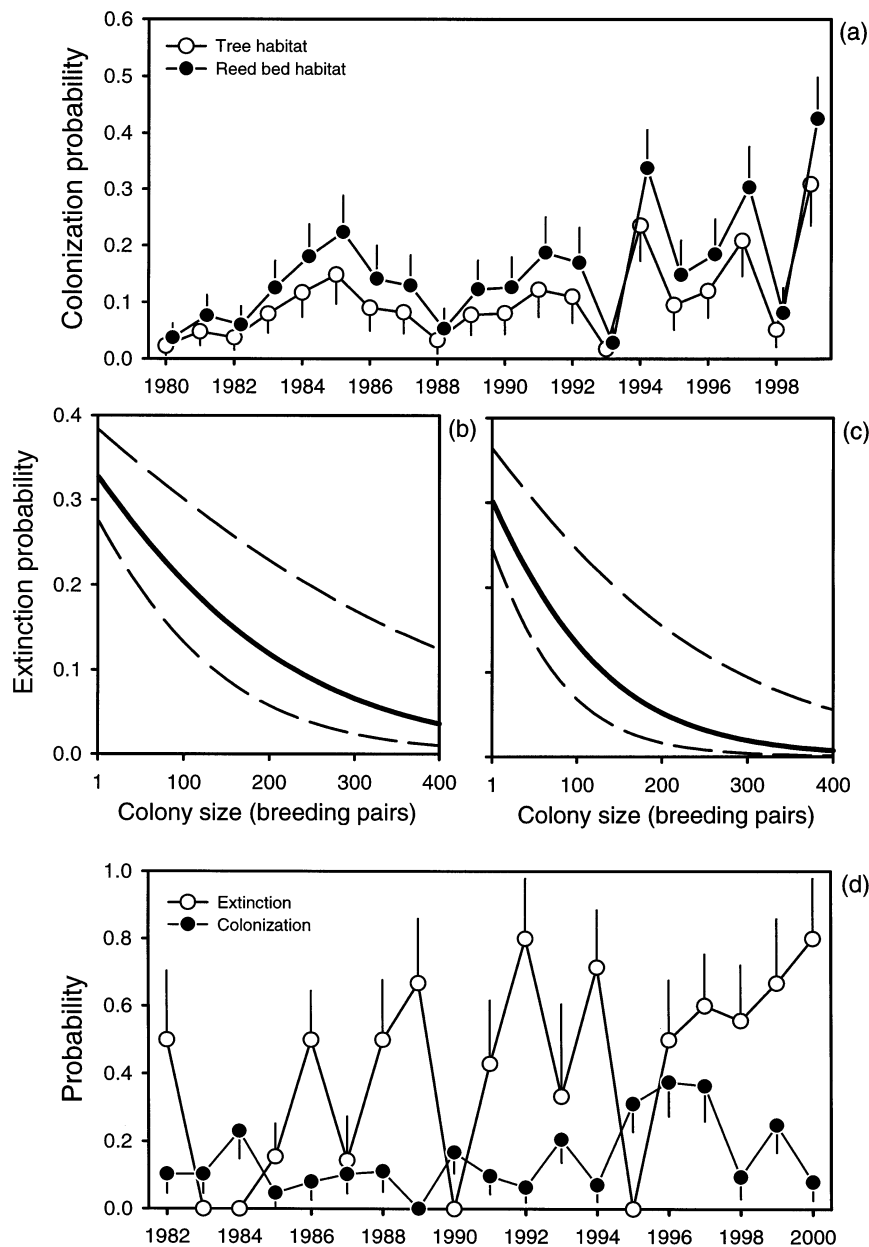
Fig. 1. (a) Parameter estimates for site colonization probabilities in grey herons using model (ϕ, γ_{h+i}) for reed bed and tree habitats. Vertical bars represent $+1$ SE; full circles represent reed bed habitat; open circles represent tree habitat. (b) Extinction probability for colony sites of grey herons and (c) purple herons as a function of colony size estimated using model $(\phi_{Siz}, \gamma_{h+i})$ and model (ϕ_{Siz}, γ_i), respectively. Plain line represents the estimated extinction probability; dashed lines represent approximate 95% confidence intervals. (c) Parameter estimates for colony extinction and colonization probabilities of purple herons using model $(\phi_{(e=w,c\times i)}, \gamma_i)$. Extinction probabilities are for the central region only, whereas colonization probabilities are for the entire study area. Vertical bars represent $+1$ SE; open circles represent extinction probability estimates; full circles represent colonization probability estimates.

survey. The corresponding model notation includes parameters for detection probabilities for sites at which colony presence had $(c_{i2}=p_{i1})$ and had not (p_{ij}) been detected previously. Finally, we were interested in the magnitudes of the detection probabilities. Specifically, if the $\hat{p}_i^*$ approach 1, then we would feel justified to reduce parameters by assuming all $p_i^*=1$. We thus evaluated several models of detection probabilities using a general parameterisation for local extinction and colonization probabilities. We then retained the selected parameterisation for detection probabilities and developed models to investigate sources of variation in colony-dynamic parameters.

Several a priori hypotheses about local extinction and colonization probabilities were incorporated into models of colony dynamics. As in the previous example, we included models in which colony dynamics did and did not behave as a first-order Markov process. Once again, our prediction was that site occupancy would indeed be state-dependent and that the probability of occupancy in year i should be higher for sites that were occupied in year $i-1$ than for sites that were not (i.e. we predicted that $\phi_i > \gamma_i$).

The different levels of reed harvesting and degrees of variability in water level for the 3 regions of the Camargue led to a priori hypotheses about both magnitudes

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and temporal variation in colony vital rates. Temporal variation was hypothesized to differ among the 3 regions, being greatest in the central region (substantial reed harvesting and water variability), intermediate in the western region (intensive reed harvesting but stable water) and smallest in the eastern region (little reed harvesting and stable water). Similarly, local extinction probabilities were hypothesized to be greatest in the central region, intermediate in the western region and smallest in the eastern region.

The detailed demographics of metapopulations are studied best using marked animals (Nichols et al. 1993, Nichols 1996). However, it is also possible to draw inferences about mechanisms underlying metapopulation dynamics using presence–absence data from a system of patches or colony sites. For example, a natural hypothesis about colony dynamics is that when extinction probabilities are high in some areas, colonization probabilities should be high for available habitat in neighbouring areas. This should be especially true when the reason for the high extinction probabilities involves habitat change (and not mortality) and movement of birds away from certain locations. The hypothesized high extinction probabilities of the central region led us to investigate models incorporating relationships between extinction probability in this region and colonization probabilities in the eastern and western regions.

For example, in model ($\phi_{(e,c,w) \times i}$, $\gamma_{(e(c),c,w) \times i}$, p), capture and recapture probabilities are equal and constant over time and region, extinction probability $(1 - \phi)$ is time-specific for each region, colonization probability (γ) is time-specific for the central and west regions, and colonization probability in the east region is modelled as a linear-logistic function of extinction probability in the central region:

$$\text{logit}(\gamma_{e,i}) = \alpha + \beta \cdot (1 - \phi_{c,i}) \qquad (2)$$

where α and β are intercept and slope parameters. The sign of the slope parameter indicates whether colonization in area e increases ($\beta > 0$) or decreases ($\beta < 0$) with

extinction probability in area c. This direct modelling of colonization as a function of extinction is preferable to a two-step approach consisting of incorporating previously estimated extinction rates for estimating colonization probability estimates, because it explicitly incorporates the sampling variance–covariance structure in model estimation and testing.

Finally, we again predicted lower extinction probabilities for larger colonies. Thus, we developed models in which extinction probability was modelled as a function of median colony size, just as in the grey heron analysis.

We started with general model ($\phi_{(e,c,w) \times i}$, $\gamma_{(e,c,w) \times i}$, $p_{(e,c,w) \times ij}$, $c_{(e,c,w) \times ij}$) that contains time-specific parameters that differ between regions (where e (east), c (central), and w (west) indicate regions) and that assumes that colony site dynamics reflect a first-order Markov process. We then used the selected parameterisation for detection probability and moved to hypotheses of biological interest (see above). Model selection was performed as for the grey heron example. Model fit, parameter estimation and testing were carried out using program RDSURVIV.

Results

Our general model, using the robust design approach, fitted the data (Table 3) and was used to build reduced-parameter models. The most simple model for capture and recapture probabilities, model ($\phi_{(e,c,w) \times i}$, $\gamma_{(e,c,w) \times i}$, $p = c$), showed the lowest AICc and fitted the data (Table 3). Under this model capture and recapture probabilities for secondary sampling periods were $\hat{p} = \hat{c} = 0.975$ ($\hat{SE} = 0.006$), leading to a high overall detection probability ($\hat{p}^* = 1 - (1 - 0.975)^2 = 0.999$, $\hat{SE} = 0.009$). Thus, as the probability of detecting breeding birds was nearly one, we modelled extinction and colonization probabilities using models with $p = c = 1$ in the interest of parsimony.

As for the grey heron, colony dynamics in the purple heron reflected a first-order Markov process. Our most

Table 3. Goodness-of-fit statistics, AICc and ΔAICc values (Δ), AICc weights (w) and number of parameters (np) for different hypotheses about time and region-specific variations in capture and recapture probabilities, using the robust design approach for purple herons in southern France. Notation for extinction and colonization probabilities were omitted because they are the same for all models (i.e. $\phi_{(e,c,w) \times i}$, $\gamma_{(e,c,w) \times i}$) used to test variation in capture and recapture probabilities. See Table 2 for explanation.

Models	Goodness-of-fit			AICc	Δ	w	np	Hypothesis
	χ^2	df	P					
($p = c$)	181.9	579	1.0	598.6	0	0.822	115	Capture and recapture probabilities identical
(p, c)	181.7	576	1.0	601.7	3.1	0.175	116	Constant capture and recapture probabilities
($p_{(e,c,w)}$, $c_{(e,c,w)}$)	240.6	570	1.0	609.7	11.1	0.003	120	Region-specific capture and recapture probabilities
($p_{(e,c,w) \times ij}$, $c_{(e,c,w) \times ij}$)	24.4	396	1.0	1790.1	1191.5	<0.001	336	Time and region-specific capture and recapture probabilities

general model for local extinction and colonization probabilities, ($\phi_{(e,c,w) \times i}$, $\gamma_{(e,c,w) \times i}$), was saturated and provided a basis for testing models that included specific constraints about time and region specificity of extinction and colonization. Model selection results presented in Table 4 provided strong evidence of time-specificity of colonization (models with constant colonization have $w < 0.001$) and of region specificity of extinction (models with only time-dependent extinction have $w < 0.001$). Support for region-specificity in colonization was weak based on w values for models with region-specific colonization. There is support for time-dependent extinction in the central region since the sum of the AICc weights for the first two models is $w = 0.841$. The estimates of extinction in the eastern and western regions were $1 - \hat{\phi}_{e,w} = 0.14$ ($\hat{SE} = 0.03$) under model ($\phi_{(e = w,c \times i)}$, γ_i), were $1 - \hat{\phi}_w = 0.11$ ($\hat{SE} = 0.03$) and $1 - \hat{\phi}_e = 0.18$ ($\hat{SE} = 0.05$) under model ($\phi_{(e,w,c \times i)}$, γ_i), and were $1 - \hat{\phi}_w = 0.11$ ($\hat{SE} = 0.03$), $1 - \hat{\phi}_e = 0.18$ ($\hat{SE} = 0.05$), $1 - \hat{\phi}_c = 0.43$ ($\hat{SE} = 0.04$) under model ($\phi_{(e,w,c)}$, γ_i). Extinction for the central region showed important variations across years (Fig. 1d) and was relatively high in some years (1992 and 2000: $1 - \hat{\phi}_c = 0.80$ ($\hat{SE} = 0.18$) and remained above 0.5 during the last six years of the study.

We used the linear-logistic function (eq. 2) to build models for which colonization probabilities in the western and eastern regions were a function of extinction probability in the central region. These linear-logistic models did not provide strong evidence that colonization in either the western or eastern region were dependent on extinction rates within the central region (Table 4). However, the estimate of β for the linear-logistic model with the lowest AICc (model ($\phi_{(e = w,c \times i)}$, $\gamma_{(w(c),e = c) \times i}$)) was positive [$\hat{\beta} = 1.47$ ($\hat{SE} = 0.82$)], suggesting that colonization probability in the western region increased with increasing extinction probability in the central region.

The model with median colony size as an individual covariate, model (ϕ_{Siz}, γ_i) where colonization was time specific and extinction was colony size-specific, had a lower AICc value (AICc = 297.99 with 21 parameters) than model (ϕ, γ_i). The ΔAICc between model (ϕ_{Siz}, γ_i) and model ($\phi_{(e = w,c \times i)}$, γ_i) was 10.01, indicating a strong effect of colony size on extinction probability as model (ϕ_{Siz}, γ_i) has $w = 0.986$. The slope parameter for the linear-logistic model was $\hat{\beta} = -1.033$ ($\hat{SE} = 0.236$), indicating that extinction probability decreased with increasing colony size (Fig. 1c).

Table 4. Goodness-of-fit statistics, AICc and ΔAICc (Δ) values, AICc weights (w) and number of parameters (np) for various models of colony site dynamics expressing different biological hypotheses about time and region annual variations in extinction and colonization probabilities, and about region annual variations in colonization probabilities as a function of region annual variations in extinction probabilities of purple herons in southern France. See Table 2 for explanation.

Models	Goodness-of-fit			AICc	Δ	w	np	Biological hypothesis
	χ^2	df	P					
($\phi_{(e = w,c \times i)}$, γ_i)	78.4	75	0.38	308.0	0	0.483	39	Time-specific extinction for c, extinction identical and constant for e and w, time-specific colonization
($\phi_{(e,w,c \times i)}$, γ_i)	75.6	74	0.43	308.6	0.6	0.358	40	Region-specific extinction, time-specific extinction for c, time-specific colonization
($\phi_{(e,c,w)}$, γ_i)	108.8	92	0.11	310.4	2.4	0.145	22	Region-specific extinction, time-specific colonization
($\phi_{(e = w,c \times i)}$, $\gamma_{(w(c),e = c) \times i}$)	80.9	73	0.25	315.6	7.6	0.011	41	Colonization in w is a function of extinction in c
($\phi_{(e = w,c \times i)}$, $\gamma_{(e(c),w = c) \times i}$)	83.9	73	0.18	319.7	11.7	0.001	41	Colonization in e is a function of extinction in c
($\phi_{(e = w,c \times i)}$, $\gamma_{(e(c),w(c),c) \times i}$)	80.5	71	0.21	319.7	11.7	0.001	43	Colonization in w and e are functions of extinction in c
($\phi_{(e = w,c) \times i}$, γ_i)	53.3	57	0.62	323.9	15.9	<0.001	57	Time-specific extinction, extinction identical for e and w, time-specific colonization
($\phi_{(e = w,c \times i)}$, $\gamma_{(e(c) = w(c),c) \times i}$)	105.3	73	0.007	325.5	17.5	<0.001	41	Colonization in w and e are identical and function of extinction in c
(ϕ, γ)	176.5	112	<0.001	346.2	38.2	<0.001	2	Constant extinction and colonization
(ϕ_i, γ_i)	109.5	76	0.006	348.5	40.5	<0.001	38	Time-specific extinction and colonization
($\phi_{(e,c,w) \times i}$, γ_i)	40.6	38	0.36	352.5	44.5	<0.001	76	Time and region-specific extinction, time-specific colonization
($\phi_{(e,c,w) \times i}$, $\gamma_{(e,c,w)}$)	81.8	54	0.009	357.1	49.1	<0.001	60	Time and region-specific extinction, region-specific colonization
($\phi_{(e,c,w) \times i}$, $\gamma_{(e,c,w) \times i}$)	–	–	–	405.8	97.8	<0.001	114	Time and region-specific extinction and colonization
($\phi_{(e,c,w) \times i} = \gamma_{(e,c,w) \times i}$)	308.0	57	<0.001	614.9	306.9	<0.001	57	Non-Markovian process

Discussion

Colony dynamics of herons in the Camargue

Our probabilistic modelling approach permitted us to investigate several models representing alternative hypotheses about heron colony dynamics in the Camargue, and several biological inferences resulted from this work. For both of our examples there was evidence that colony dynamics were best represented as a stochastic Markov process. The probability that a colony site was occupied at time i depended on whether the colony site was occupied at time $i-1$. As predicted, estimated probabilities of occupancy in i given occupancy in $i-1$ ($\hat{\phi}_i$) were generally higher than estimates given non-occupancy in $i-1$ ($\hat{\gamma}_i$). This evidence of fidelity to previous colony sites was expected, but we note that similar modelling approaches produced no such evidence for another species of colonial water bird, gull-billed terns in coastal Virginia (Erwin et al. 1998).

The model sets for both *A. cinerea* and *A. purpurea* were based on a priori hypotheses about likely sources of variation in extinction and colonization probabilities. For the grey heron, extinction was relatively constant throughout the study period and did not vary with habitat type (reed bed or tree). However, the modelling provided evidence that extinction probability was higher for small than for large colonies as predicted on several grounds (e.g. demographic stochasticity, conditional [on previous success] fidelity, active habitat selection with low to moderate temporal variation in habitat quality, social attraction or facilitation). By contrast with extinction, colonization probabilities in the grey heron differed between habitat types and years, with an overall increase in probabilities during the study and higher probabilities in reed beds than in trees. These results illustrate the observed habitat change (from trees to reed beds) and increase in numbers of breeding grey herons during the last 20 years in the Camargue (Kayser et al. 1994, Thomas and Hafner 2000).

For the purple heron, distinct regional patterns of colonization and extinction were found, with higher and more variable extinction rates within the most intensively managed region (up to 80% of the colonies went extinct in some years), as predicted. The fact that extinction rates remained consistently high during 1996–2000 probably also reflects the increasing harvesting pressure on reed beds during these years (Barbraud and Mathevet 2000). As with the grey heron, the modelling provided some evidence of the predicted higher extinction probabilities for smaller colonies of the purple heron. The approach of directly modelling colonization probabilities of sites within some regions as a function of extinction probabilities for colonies in neighbouring regions provided only weak evidence of the predicted relationship. However, we believe that this approach may be a reasonable way of dealing with the fact that breeding individuals move from one area to another when individual marking is not an appropriate way to address this problem.

Modelling methodology

Modelling extinction and colonization probabilities using a probabilistic framework permitted us to draw separate inferences about sources of variation in these parameters, which would have not been possible using a simple turnover index combining both extinction and colonization. In addition, this type of modelling was useful for investigating whether colony site use was affected by state variables such as colony size and by covariates such as habitat type. Although our examples included only bird species, the analysis of colony dynamics using these approaches is not restricted to avian species. Colonial breeding is also found among other vertebrate species and is widespread among invertebrates. The modelling approaches developed here can also be used for estimating extinction and colonization probabilities of sites used by other types of breeding (leks) or non-breeding (roosts) aggregates of individuals.

Our approaches to estimating extinction and colonization probabilities at colony sites require the assumptions of the Cormack–Jolly–Seber (CJS) and robust design approaches. Heterogeneity of detection probabilities and community-level vital rates has not been explored in these models, although results for estimation of survival in capture–recapture models are encouraging (Carothers 1973, 1979; Nichols et al. 1982; Pollock et al. 1990). The assumption of no tag loss in CJS modelling simply translates into an assumption that the different colony sites are recognized and properly identified each year. The existence of modern Global Positioning System equipment and Geographic Information System software should ensure that this assumption is easily met. CJS modelling assumes independence of fates of individuals (Seber 1982). In our case this implies that all colony sites must be independent, at least with respect to occupancy characteristics. This assumption may be violated when subcolonies exist within a given area unit and where the subcolony sites are treated as separate sites. To minimize this potential problem, colony sites may be defined based on local knowledge of the ecology of the studied species (i.e. existence of subcolonies) and on known environmental variation within habitats units.

Kendall (1999) reviewed the implications of violation of the closure assumption of the robust design approach and identified scenarios where the estimation of p^* would still be unbiased. In our situation, the closure assumption may be violated when birds start breeding at some sites or when breeding birds abandon a site between two secondary samples. Many colonial species

are highly synchronous and colonies may indeed settle in a short time interval (one or two days). To avoid violation of this assumption, the interval separating the secondary sampling sessions should be sufficiently small to ensure that birds do not all start breeding or stop breeding at some sites in between. If it is not possible to meet the closure assumption for secondary periods, then multiple (at least 3) secondary sampling occasions can be used in conjunction with open models (Schwarz and Stobo 1997).

Our example analyses assumed that colony sites did not disappear during the course of the study. However, we indicated how this assumption can be relaxed by including a survival parameter for the sites themselves. Thus "censoring" of sites is easily incorporated into the analysis.

For both of the examples presented here the most general model fitted the data adequately. In cases where no model fits the data well, it might be appropriate to compute a variance inflation factor based on the goodness-of-fit test results and use a quasi-likelihood approach (Burnham et al. 1987, Lebreton et al. 1992). As Nichols et al. (1998), we emphasize that lack of model fit is not an adequate reason for abandoning an estimation approach and resorting to the use of a simple turnover metric, because model-based estimates will probably exhibit less bias than a turnover metric, even when model assumptions are not met.

In addition to estimating colony site extinction and colonization probabilities, the approaches described here should be useful in designing monitoring programs for population or colony abundance when the investigators are not certain whether all colonies are detected. Initially the monitoring program could be conducted under the robust design approach with two or more secondary sampling periods in order to estimate the detection probability of colonies. Based on this estimate a decision can be made whether to reduce survey efforts to one sampling occasion in the case where all colonies are detected, or to continue with multiple sampling occasions when a substantial proportion of colonies is missed. In the case where some colonies are undetected, the effects of relevant covariates (e.g. vegetation characteristics, habitat type, colony size) on detection probabilities can be tested. For example, the *A. purpurea* data indicated that if only one aerial survey was conducted every year about 2.5% of the colonies would be missed, and further modelling indicated that smaller colonies ($< 5-6$ breeding pairs) were more likely to be missed ($\hat{p} = 0.97$) than larger ones ($\hat{p} = 0.99$). The state variable for such a monitoring program would be the proportion of sites occupied by colonies each year (denote this quantity as ψ_i for year i). If the number of sites at which breeding birds are detected in year i is denoted as n_i, then the proportion occupied can be estimated as:

$$\hat{\psi}_i = \frac{n_i}{\hat{p}_i^*}.$$

Dynamic models such as those presented here can be reparameterised to directly estimate rate of change in the state variable, ψ_i, as is done for animal abundance in standard capture–recapture modelling (Pradel 1996).

Although our two examples involved colonies of breeding birds, we believe that there are some natural extensions of our approaches to the metapopulation and community levels. The concept of metapopulation considers the dynamics of a number of sub-populations that exchange migrants and that may be subject to local extinction and recolonization (Levins 1969, Hanski and Gilpin 1991). In metapopulations, patch occupancy and persistence are functions of extinction and colonization rates, and estimating those rates is a primary goal of metapopulation studies. For field situations in which all sub-populations present in an area are detected at each sampling occasion, the first approach presented above can be used to estimate rates of extinction and colonization of sub-populations within habitat patches (Clark and Rosenzweig 1994, Rosenzweig and Clark 1994). However, for certain species or groups of species there might be sampling situations where sub-population detection probabilities are < 1, in which case estimators of vital rates based on complete detection will be biased. In such situations the estimation methods developed here using the robust design approach may be useful to estimate those rates, to estimate sub-population detection probabilities, and to investigate the potential influence of environmental and management factors on those rates. We are aware of a number of field studies on metapopulation dynamics in which sub-populations are distributed among discrete habitat patches that can be easily identified and characterized. For example, most amphibian metapopulation studies take a "pond-as-patches" approach to metapopulation dynamics (Marsh and Trenham 2001). These authors also highlighted the methodological problems linked to detection probabilities and biological processes when estimating extinction and colonization probabilities using a simple turnover metric.

Our approaches should also be useful for analysing species dynamics in an area. Nichols et al. (1998) developed a method based on probabilistic capture–recapture models for estimating local species extinction, colonization and turnover in animal communities when the average detection probability for a group of species is < 1. They noted, "…it would be possible to restrict interest to specific subset of species (guilds or taxonomic groups)". In fact the approach we develop here can be used for a finer scale analysis as species-specific detection probabilities and extinction/colonization rates can be estimated when a network of sites are surveyed regularly and presence/absence of individual species of interest is recorded. The disadvantage of our approach

is that it may require a higher level of efforts than the method developed by Nichols et al. (1998).

Finally, our approaches may be used for estimating colony abundance (or sub-population abundance in the case of metapopulations). For example, when a monitoring program for colony abundance covers a large area, it should be possible to estimate colony detection probability using the robust design approach over a predefined sampling frame. Detection probability can then be incorporated into abundance estimators from data collected over the sampling frame in order to obtain unbiased estimates of abundance for the entire area (Thompson et al. 1998, Yoccoz et al. 2001).

To conclude, the approach assuming perfect detection (Erwin et al. 1998) should be useful for estimating extinction and colonization probabilities of colony sites when all colonies present are detected at each sampling occasion. In situations where colony detection probabilities are < 1, the second estimation method described here using the robust design approach should be useful. Estimation methods developed here for analysing colony site dynamics may also be extended to analysing metapopulation and species dynamics.

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