

Exploiting uncertain ecological fieldwork data with multi-event capture–recapture modelling: an example with bird sex assignment

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Summary

1. Sex plays a crucial role in evolutionary life histories. However, the inclusion of sex in demographic analysis may be a challenge in fieldwork, particularly in monomorphic species. Although behavioural data may help us to sex individuals in the field, this kind of data is unlikely to be error free and is usually discarded.

2. Here we propose a multi-event capture–recapture model that enables us to exploit uncertain field observations regarding the sex of individuals based on behavioural or morphological criteria. The multi-event capture–recapture model allows us to account for sex uncertainty not restricting our ability to estimate the parameters of interest. In this case, by adding the confirmed sex of just a few individuals, we greatly improve the efficiency of the optimization algorithm.

3. Using such an approach, we analysed sex differences in demographic parameters (e.g. survival, transience and sex ratio) in a population of Audouin's gulls using observations from long-term fieldwork monitoring (1988–2007). We also assessed the probability of ascertaining sex over time and the probability of error for each field-sexing criterion.

4. We detected no strong effect of sex on either survival or transience probabilities, and both sexes showed a decreasing trend in survival over time and transience probability after recruitment increased with age and over time. The probability of ascertaining sex over time depended on observers' experience. Strikingly, courtship feeding (but not copulation) emerged as the most reliable clue for sexing individuals, which would suggest that Audouin's gulls engage in same-sex sexual behaviour such as same-sex mounting.

5. The present modelling emerged as a reliable method for estimating demographic parameters and state transition parameters in ecological studies in which field observations of sex or other individual states are assigned erroneously and uncertainly. This approach could also be useful for applied ecologists for assessing the reliability of their criteria for assigning sex or other individual covariates in the field, thereby permitting them to optimizing their field ecological protocols.

Key-words: fieldwork, multi-event capture–recapture, sex assignment, survival probability, uncertainty

Introduction

Sex is one of the main individual features shaping life-history traits in most organisms. It is known to influence survival, dispersal, recruitment and other life-history parameters that have important consequences for demography and population dynamics (Greenwood 1980; Stearns 1992; Gowaty 1993; Clobert *et al.* 2001). Thus, it is essential to assess the potential effects of sex in ecological and evolutionary studies

(Krebs 2001). However, incorporating sex into these studies depends on the ability to assign sex with certainty. Difficulties may appear when studying monomorphic or slightly dimorphic species that are monitored in the field from a distance and when direct manipulation for gonadal inspection, biometrical or acoustical discrimination, or molecular sexing is not possible; in such cases, field biologists often rely on sexual behaviour (e.g. courtship, copulation) to distinguish males from females (e.g. Moynihan 1955; Bustnes *et al.* 2000). In these cases, it may occur that an animal that has once been recorded as a male may be later referred to as a female or vice

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versa (Pradel *et al.* 2008). This is because some of the behavioural criteria used in the field are wrongly assumed to be totally reliable or because some criteria are more prone to field observation errors. When such potential biases are recognized, field biologists tend to either refuse to estimate sex-specific parameters or to analyse only those individuals whose sex has been determined with a reasonable degree of certainty, thereby also leading to biased sampling (e.g. if the accuracy of sexing changes with animal age or condition). However, in the latter case, many individuals included in the data set have to be discarded (for instance, Pradel *et al.* 2008 discarded up to 80% of the total data set) owing to uncertainty regarding their sex assignment (Nichols *et al.* 2004). Another option is to use animals that have not been sexed as a third group, but this approach yields biased (i.e. overestimated) demographic parameters for the two sex groups, because animals assigned to these groups are likely to have survived longer (i.e. to have been observed on more occasions) (see Oro, Pradel & Lebreton 1999; Nichols *et al.* 2004; Pradel *et al.* 2008). To overcome this bias, Oro & Pradel (2000) proposed that the survival of the unknown-sex individuals be considered as a weighted average of the survival of the two sexes, with the weights reflecting the proportions of males and females among the animals of uncertain sex. However, this method presupposes the existence of a given sex ratio in the population and does not use all the information available from field observations. Finally, Nichols *et al.* (2004), in an attempt to overcome the fact that survival estimates for animals of known sex are positively biased, proposed a reliable multistate model approach with probabilistic transitions from unknown sex to known sex.

Nichols *et al.* (2004) showed that it is possible to estimate sex-specific demographic parameters such as survival when the sex is not known for all individuals. Nevertheless, these authors also acknowledged that their method relied on the assumption that animals were assigned to a specific sex with certainty. Furthermore, in most cases, the certainty of assigning sex increases with the number of times an individual is recaptured or resighted, and thus, sex is known with a higher degree of certainty for individuals who do not disperse permanently or for those that live longer (see Nichols *et al.* 2004). Pradel *et al.* (2008) developed the first capture–recapture survival model to account for uncertainty in the assessment of sex: they examined parameter redundancy and the usefulness of incorporating the least reliable sexing clues and the genetic determination of sex available for only a handful of individuals as a means of improving the efficiency of the optimization algorithm (see also Conn & Cooch's (2009) application to disease modelling). Given that its efficiency has been proven, here we further develop this multi-event capture–recapture modelling to examine sex differences in a number of demographic parameters, namely survival and transience, as well as to analyse the sex ratio in the population. In other words, here we formulate a new parameterization and extend the multi-event model described by Pradel (2005). Contrary to Nichols *et al.* (2004), we treat the problem of reliability in the criteria used to sex individuals by

estimating the probability of error for each field-sexing criteria, as well as the probability of judging (assigning sex) over time. Additionally, we explore the sexual behaviour of the study species during its reproductive season. For these purposes, we used a large, long-term capture–recapture data set for Audouin's gull *Larus audouinii*, a monomorphic species breeding in the Ebro delta in the western Mediterranean, where 65% of the world's breeding population occurs. Although the demography and population dynamics of this population have been studied in depth (e.g. Oro & Pradel 1999, 2000; Oro, Pradel & Lebreton 1999; Oro & Ruxton 2001; Cam *et al.* 2004; Oro *et al.* 2004; Tavecchia *et al.* 2007), few such analyses (except Oro, Pradel & Lebreton 1999) have ever considered the potential effects of sex given the inherent difficulties in distinguishing the sex of breeding birds.

Materials and methods

FIELDWORK DATA AND PROTOCOL

From 1988 to 2004, 15 765 chicks were marked (mean = 927 chicks/year, SD = 430) in the colony, and the data set covers 14 years of monitoring (1994–2007). Marking birds as chicks is much easier than capturing adults and allowed us to test for the effect of age on demographic parameters. However, sexes are only distinguishable using molecular techniques (Genovart *et al.* 2003a), a method that is impractical for a large number of birds. In addition, the recapture of marked birds was conducted at distance (i.e. resights of darvic rings with an alphanumeric code using a spotting scope) and so most adults were never manipulated, a practice that would have allowed us to use biometrics to conclusively ascertain their sex (Genovart, Oro & Bonhomme 2003b; Genovart *et al.* 2003a). This constraint is common to many studies of species with little sexual dimorphism, both when marking chicks and identifying adults. Thus, during fieldwork we recorded behavioural information to ascertain sex whenever possible, mostly during the occupancy and pre-laying stages when birds exhibit courtship display such as begging for food (assuming that females beg for food from males before copulation), courtship feeding (assuming that males feed females before copulation) and copulation (by indicating either a male or a female depending on whether the bird was on top or below) (see Oro 1998). We also used the imperfect clue of body size when both members of the pair were close together, males being ca. 15% larger than females (Genovart, Oro & Bonhomme 2003; Genovart *et al.* 2003a,b). When an individual was observed several times during the same season, priority for coding was given to the criteria in the following order: copulation, courtship feeding, begging food and relative body size. To test several hypotheses regarding the clues used in this kind of study, we also used information from some birds that were sexed conclusively, that is, chicks and adults (captured during incubation) that were sexed with molecular techniques or biometrics as part of one or more behavioural and population studies (Genovart, Oro & Bonhomme 2003; Genovart *et al.* 2003a,b). This allowed us to develop more realistic models in a step forward from the previous study by Nichols *et al.* (2004) on the estimation of sex-specific survival in the case of uncertainty in sex assignment (for an assessment of the usefulness of some molecular sexing in multi-event modelling of sex uncertainty, see also Pradel *et al.* 2008). As we resighted breeders every year, some birds could be sexed several times during the study and thus we

could test for (i) consistency in sex assignment, (ii) the probability of misjudging the sex of a breeder using a given criterion and (iii) the usefulness of gathering even the least reliable clues. We considered all the criteria, including those that in theory are assumed to be inconclusive (such as begging for food during courtship, see Nichols *et al.* 2004) or definitive (such as copulation), in an attempt to assess how reliable they are.

MULTI-EVENT CAPTURE-RECAPTURE MODELLING

The encounter history data only included gulls observed at least once as sexually mature gulls (with an age ≥ 3 years). We used the multi-event framework to estimate demographic parameters from data gathered under a field protocol in which sex was assigned with some degree of error. This framework is one of the most recent developments in capture-recapture models and was specifically designed to deal with uncertainty in the collection of capture-recapture data. A formal description and technical details of these models can be found in Pradel (2005) and Pradel *et al.* (2008). The main idea of the multi-event approach is that there are two levels in capture-recapture data: a directly accessible level called the 'events', which are encoded in the capture histories, and another level that can only be inferred but which is of primary interest, namely the 'states'. These states change over time according to a Markov process. The events are generated from the states on each occasion. For the study of sex uncertainty, we consider three states: 'live male present in study area', 'live female present in study area' and 'dead individual or transient' with no transition allowed between the first two. Transients are individuals that show up only once in the colony and thus are never seen again; Tavecchia *et al.* (2007) showed that many of these birds dispersed permanently to other colonies within the metapopulation. The state process is governed by survival probabilities, traditionally denoted ϕ in the capture-recapture literature, while the proportion of transients is denoted τ in each sex (see Fig. 1); thus, τ parameters only apply for the time interval after first capture. For instance, a live male at time t that is a transient or dies before the next season will be in the 'dead or transient' state at time $t + 1$ [probability $\tau + (1 - \tau)(1 - \phi)$]; otherwise, it remains in the 'live male' state [probability $(1 - \tau)\phi$]. The first time an individual is observed breeding, its state is either 'live male' or 'live female'. The probability of being a live male or a live female depends, among other things, on the sex ratio in the population. The probability of the initial state is another parameter of the multi-event models. The greatest challenge here is to describe the complex observation process (see Fig. 2). When an individual is encountered (with probability P), there is some chance that it will be sexed (σ) based on its general appearance (body size: probability β) or its behaviour (probability $1 - \beta$). When behaviour is used, there are three different criteria (copulation, begging for food and courtship feeding), which occur with probabilities x_1 , x_2 , and $1 - x_1 - x_2$ (' x_3 '), respectively. Finally, each criterion has its own reliability (probabilities ρ_1 , ρ_2 , ρ_3 , ρ_4 , where ρ_4 is the reliability of the body-size criterion). For more detailed information on specific multi-event modelling of sex uncertainty, see Appendix S1.

At this stage, we distinguished three groups based on birds' age (given in years) when they were first recaptured when breeding: 3 or 4; 5, 6 or 7; and > 7 , as previous analysis has revealed that the proportion of transients tends to increase with recruitment age (Tavecchia *et al.* 2007). There is no goodness-of-fit test available for multi-event models at the moment. Thus, we assessed the fit of a model that only retains information regarding whether an individual is encountered or not (Cormack-Jolly-Seber type models). We used U-CARE (Choquet *et al.* 2009) to assess the fit of the

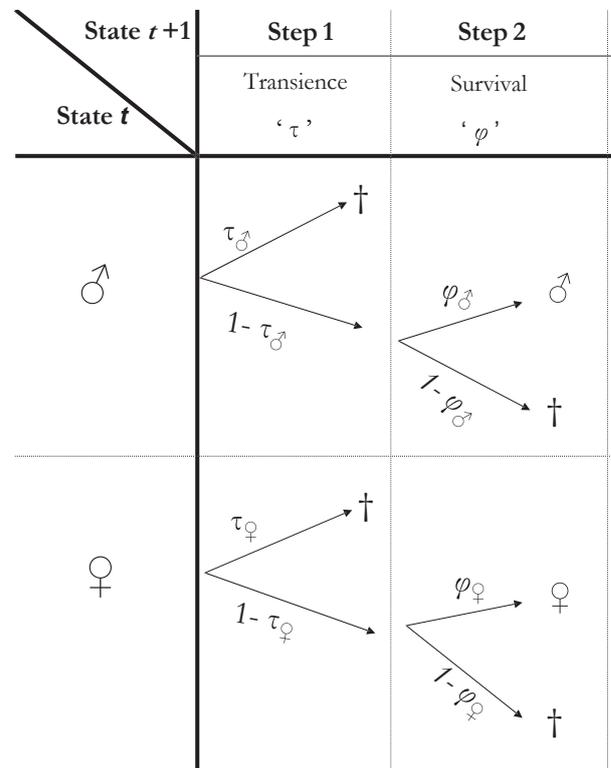


Fig. 1. Transitions between state at t and state at $t + 1$ for each sex of Audouin's gull during the study. † represents the state 'dead or transient'; ♂, the state 'live male'; and ♀, the state 'live female'.

Cormack-Jolly-Seber model by groups and paid special attention to the Test 3.SR component that detects the presence of transients (Pradel *et al.* 1997). In our data set of 7048 individuals, 846 were seen only once (12.0% of total individuals; see results), of which 258 were seen at the other 13 breeding sites where monitoring is also being conducted. This number is a minimum number that should increase once it has been corrected for resighting probabilities at these other sites. On the basis of GOF test results, we calculated a variance inflation factor to be used in the models. This is conservative as the goodness-of-fit test is for a more general model with stronger assumptions (e.g. no sex or age differences).

For the analysis, we took into account the known sex of those individuals sexed by either of the two methods – genetic or biometric – that we consider to be thoroughly reliable. For this purpose, we classified the individuals into groups based on the combination of birds' ages at first resighting and the knowledge of their sex (unknown, known males and known females). As reliable sexing was not used early in the study, there were no individuals of known sex among the first birds resighted at more than 7 years, and so we ended up with seven groups (see Appendix S1). For known males, the initial state probability of being a male was set to 1; for known females, it was set to 0. For the remaining groups of individuals of unknown sex, the initial state probability was left unestimated. Although survival has already been analysed in previous studies (Oro, Pradel & Lebreton 1999; Tavecchia *et al.* 2007), the difference between females and males was not tested. We considered sex specificity and tested whether the frequency of sexing based on relative body size increased over the years as compared to the use of behavioural cues. This was based on our impression that there was an increasing trend to use the body-size criterion as observers gained experience and confidence over time. The relative use of each behavioural criterion depends

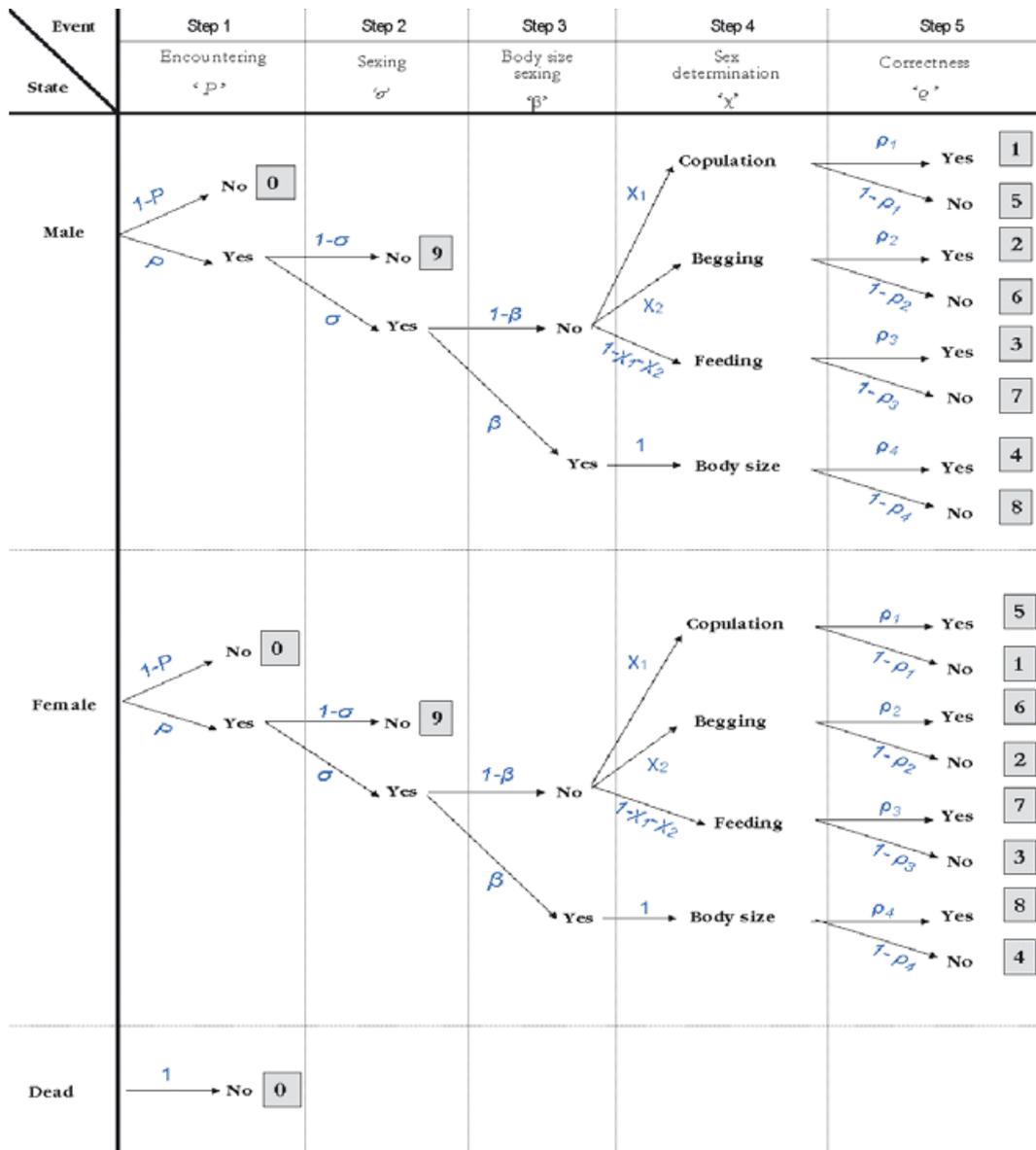


Fig. 2. Codes used for each event (numbers within squares) in multi-event modelling integrating sex determination information for Audouin's gulls in our study.

essentially on the proneness of animals to engage in the corresponding activity. As there is no reason to assume that this changed over time, we kept x_1 , x_2 and x_3 constant. Additionally, because all four methods of sexing from observations require the presence of both members of the pair, the chance of sexing males and females in each case was considered to be equal.

We tested the different effects considered by fitting the corresponding models to the program E-SURGE (Choquet, Rouan & Pradel 2009), which uses a quasi-Newton algorithm for optimizing the likelihood. Model selection relied on the Akaike Information Criterion corrected for over-dispersion and small samples sizes (QAICc, Burnham & Anderson 2002).

Results

From 1994 to 2007, we performed 57 757 resightings of Audouin's gulls in the Ebro delta colony, corresponding to

7048 capture–recapture histories of breeding birds (observed at least once with an age ≥ 3 years). The mean number of observations per individual was 3.25 (SD = 2.60; range, 1–14). We assessed the sex of only 1.4% ($N = 99$) of the resighted birds using methods that we consider to be sure (see Methods), while for 22% ($N = 1541$) of the remaining birds, we applied one or several of the other criteria. Copulation was observed in 130 individuals, begging for food in 753 and courtship feeding in 152, and body size was assigned in 506 individuals. For the 1541 individuals for which an uncertain sex was assigned, 217 had their sex assigned on two or more occasions. Of these birds, 89% of multiple assignments were consistent within individuals between years and only in 23 cases were birds sexed as males and females in different years.

The global goodness-of-fit for the Cormack–Jolly–Seber type model (distinguishing three groups based on age at first

recapture) was poor ($\hat{c} = 974.88/170 = 5.7$), probably due to a transient effect. After removing the first encounter and thus eliminating all potential transients, we achieved an acceptable variance inflation factor, $\hat{c} = 1.84$ (262.69/143). Thus, we fitted models incorporating the presence of transients and corrected for the remaining lack of fit by scaling the model deviance with this last variance inflation factor. The use of this variance inflation factor was conservative, because our model had more structure than a normal CJS model (Pradel 2005).

Model selection is summarized in Table 1: the models with the highest Akaike weight revealed a clear effect of time on survival and recapture probabilities, along with an effect of time and age at first resighting on the transience probability. As the two first models had very similar support ($w = 0.47$ and $w = 0.37$; Table 1), we show model averaged parameter estimates. Recapture probability was mostly high and varied over the study period (1995–2007), ranging from 0.49 (95% CI, 0.45–0.53) to 0.90 (0.88–0.92) (Fig. S1). Adult survival

probability also varied over time, and models including a decreasing trend in survival over the years clearly reduced the QAICc value (Table 1 and Fig. 3). The average adult survival rate was estimated at 0.88, ranging from 0.85 to 0.91. We did not detect a strong effect of sex on survival probability, even though the second best-ranked model at only 0.5 AIC points, included such effect, with females showing a slightly higher survival rate than males (0.890; 95% CI, 0.874–0.903, and 0.876; 95% CI, 0.859–0.891, respectively). Transience probability also varied with time and age at first resighting (see Table 1 and Fig. 4); for individuals first seen at 3 or 4 years, such probability was very low, averaging 0.036 (95% CI, 0.02–0.07) and did not change over the study period. For individuals first resighted at 5–7 years, the transient probability increased over time, averaging 0.39 with a minimum of 0.013 in 1994 and a maximum of 0.71 in 2004. For individuals first resighted at more than 7 years, transient probabilities were even higher, averaging 0.59 with a minimum of 0.39 in 1994 and a maximum of 0.89 in 2004. Even

Table 1. List of the 15 models with lowest QAICc values. Model structures were decided following methods described in Tavecchia *et al.* 2007.

No.	Np	Deviance	QAICc	Δ_i	w_i	Hypotheses tested	
						On survival	On transient
1	65	57250.32	31414.71	0.00	0.47	Linear trend with time	Effect of age at first resight Effect of time only for birds first resighted at ages older than 4 year
2	66	57247.57	31415.21	0.51	0.37	Linear trend with time and sex. Equal slope for both sexes	Effect of age at first resight Effect of time only for birds first resighted at ages older than 4 year
3	67	57246.99	31416.91	2.21	0.16	Linear trend with time and sex. Different slope for each sex	Effect of age at first resight Effect of time only for birds first resighted at ages older than 4 year
4	78	57236.20	31433.16	18.45	0	Linear trend with time	Effects of sex and age at first resight Effect of time only for birds first resighted at ages older than 4 year
5	79	57233.84	31433.88	19.17	0	Linear trend with time and sex. Equal slope for both sexes	Effects of sex and age at first resight Effect of time only for birds first resighted at ages older than 4 year
6	88	57207.31	31437.51	22.81	0	Change with time	Effects of sex and age at first resight Effect of time only for birds first resighted at ages older than 4 year
7	90	57203.07	31439.23	24.53	0	Change with time and sex Different for each sex	Effects of sex and age at first resight Effect of time only for birds first resighted at ages older than 4 year
8	79	57275.38	31456.58	41.87	0	Change with sex	Effects of sex and age at first resight Effect of time only for birds first resighted at ages older than 4 year
9	78	57280.21	31457.21	42.50	0	Constant	Effects of sex and age at first resight Effect of time only for birds first resighted at ages older than 4 year
10	77	57291.50	31461.36	46.65	0	Constant	Effect of age at first resight Effect of time only for birds first resighted at ages older than 4 year
11	54	57528.47	31544.59	129.88	0	Constant	Effects of sex and age at first resight
12	52	57623.69	31592.60	177.89	0	Effect of age	Constant
13	53	57621.03	31593.16	178.45	0	Change with sex	Effect of age
14	54	57618.05	31593.54	178.83	0	Constant	Effect of age at first resight
15	52	58104.77	31855.49	440.78	0	Change with sex	Effect of sex

Note that not all relevant models are shown here. Notation, Δ_i , the QAICc difference between the current model and the one with the lowest QAICc value; Np, number of parameters; w_i , weight of model i . The selected model is in bold. In all models shown the recapture probabilities vary over time.

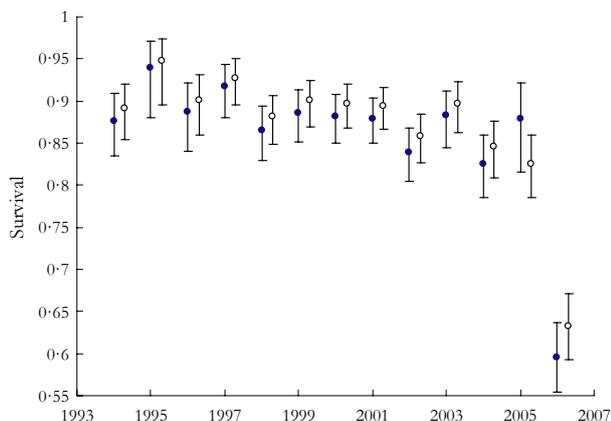


Fig. 3. Estimates of survival probabilities for Audouin's gull in males (solid dots) and females (open dots) in the Ebro delta from the time-dependent model (see Table 1). Note that the best-ranked models show a linearly declining survival trend.

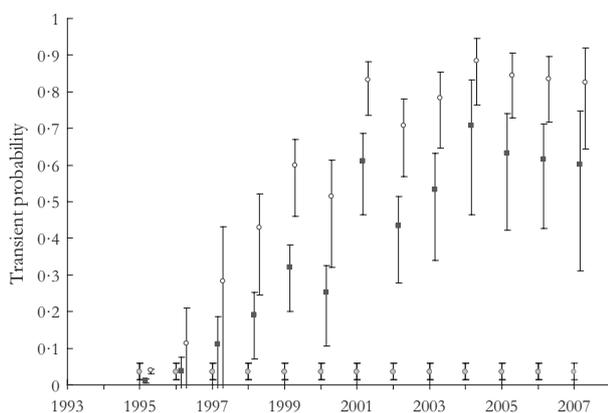


Fig. 4. Estimates of transient probabilities for Audouin's gull in the Ebro delta during the study period from the best-ranked model (see Table 1). Transient probabilities depended on age at first resighting and time for individuals first resighted at more than 4 years, being lower in individuals first seen at 5 and 7 years (in solid squares) than in individuals first seen at more than 7 years old (in open dots). In individuals first seen at 3 and 4 years (in grey dots), transient probabilities were very low, averaging 0.036 (CI 95%, 0.02–0.07) and did not change over the study period.

though we could not exclude the possibility that the sex ratio in this population was slightly skewed towards females (49% males), 95% confidence intervals (0.44–0.53) do support parity in the sex ratio in sexually mature Audouin's gulls.

We found variation over time in the probability of sex assignment and in the use of body-size criteria for sexing (Table 2). The probability of misjudging the sex of a breeder relied on the criterion used (Table 2); surprisingly, the copulation criterion did not emerge as the most reliable criteria for sexing birds by behavioural clues in the field; courtship feeding was the most reliable criterion, with no error detected over the study period and no overlap in the 95% confidence intervals with the other criteria. Body size was the least reliable criterion, with about a 9% error probability (Table 2), but its accuracy increased in the final years and could be employed throughout the breeding season.

Table 2 Frequency of use of each sex criterion, probability of sex assignment by each criterion from 1994 to 2007 and probability of error when applying each criterion. The frequency for the behavioural criteria is calculated conditionally on observed behaviour (total = 1). We used the model with the highest Akaike weight (see Table 1), i.e., the model with (i) constant recapture probabilities over the study period, (ii) equal survival probability between sexes and with a linear time trend and (iii) transience probability depending on age group (> 4 year) and time

Sex criterion		Frequency of use (95% CI)	Prob. of error (95% CI)
Copulation	Constant	0.12 (0.10–0.16)	0.04 (0.038–0.044)
Begging for food	Constant	0.73 (0.69–0.76)	0.05 (0.02–0.11)
Courtship feeding	Constant	0.14 (0.11–0.19)	0 (0.0–0.01)
Body size	Time dependent	0.29 (0.00–0.72) ^a	0.09 (0.04–0.18)

^aAs the probability of sexing using the body-size criterion in the best model is time dependent, here we give the mean value with the minimum and maximum value between parentheses.

Discussion

It is known that some life-history traits such as adult survival and recruitment may be sex specific (Jon *et al.* 1997; Weimerskirch, Barbraud & Lys 2000; Tavecchia *et al.* 2001, 2002; Wilkin & Sheldon 2009; Oro *et al.* 2010; Ramp *et al.* 2010; Millon *et al.* 2011), and thus, the incorporation of sex as an individual covariate enables sex-specific biological hypotheses to be tested (e.g. Payevsky *et al.* 1997; Nichols *et al.* 2004; Oro *et al.* 2010; Teplitsky *et al.* 2010). This is crucial in the study of population dynamics and for predicting reliably, for instance, the probabilities of extinction in species with sex-specific demographic traits or, more particularly, in those with non-monogamous mating systems (Caro 2007; Bessa-Gomes, Legendre & Clobert 2010). A further example is the appearance of trios in the mating systems of some bird species (e.g. Mills 1989; Szczys *et al.* 2001; Carrete *et al.* 2006; Genovart *et al.* 2008), which has also increased interest in the evolutionary and ecological consequences of skewed sex ratios in populations and their dynamics (e.g. West & Sheldon 2002). It is thus important to develop new methods for taking sex into account even if the clues for sex identification are not always perfect (Nichols *et al.* 2004). Here we show that multi-event models allow us to analyse the effect of sex on survival and transient probabilities as well as the sex ratio in the population of a species where sex cannot be easily determined. We used imperfect field data that would otherwise have been discarded. Although it is always desirable to employ a method with no error (in our case molecular sexing of some birds), the lack of such a method does not preclude the estimation of other parameters (see Pradel *et al.* 2008, Table 5). To emphasize this idea, it can be calculated that in our study, one instance of sex assessment from a highly, say 98%, reliable criterion is equivalent to two consistent

observations of an 88% reliable criterion or three consistent observations of a 79% reliable criterion. A 90% or more criterion is thus an excellent criterion (all of the ones we used enter this category) and a > 80% reliable criterion a good one. Thus, the method will still be reliable even if only uncertain data are used. This should be the case for most of studies using available mark-recapture data based only on observational or morphometric criteria for sexing individuals.

We assessed the probability of ascertaining sex over time, which depended on observers' fieldwork experience and the probability of error inherent for each field-sexing criterion. In terms of courtship behaviour, courtship feeding (and surprisingly not copulation) emerged as the most reliable clue for sexing Audouin's gulls. Some of the detected errors associated with copulation probably reflect homosexual behaviour in this species, and indeed, all kinds of same-sex sexual behaviour, from elaborate courtship displays to mounting and genital contact, have been noted in other bird species (MacFarlane *et al.* 2007; Young, Zaun & VanderWerf 2008). For many species, and particularly for socially monogamous species, females pairing with other females and co-parenting while seeking extra-pair reproductive chances with paired males could be a beneficial strategy (MacFarlane *et al.* 2007). In the same context, Young, Zaun & VanderWerf (2008) documented the long-term pairing of unrelated female Laysan albatrosses *Phoebastria immutabilis* and showed how cooperation may have arisen as a result of a female-skewed sex ratio in this species. Our study suggests that Audouin's gulls may also engage in same-sex sexual behaviour, same-sex mounting being more frequent in this species than same-sex courtship feeding. This might be due to the relatively high cost of courtship feeding (Drent & Daan 1980). However, we cannot exclude the possibility that the observed error was partially due to reverse mounting, as has been observed in other bird species (e.g. Ortega-Ruano & Graves 1991; Wagner 1996). In the absence of typical pre-laying courtship behaviour, only body size appeared as a sexing criterion for Audouin's gulls. Our models confirmed that the body-size criterion was associated with the highest error probability. The use of such a criterion requires fieldwork experience that can only be acquired over the years (i.e. the error decreased in the final years), although it is still worth using this criterion, especially because it can be employed throughout the breeding season.

Differences in survival between sexes tend to be small in monomorphic or slightly dimorphic bird species (Promislow, Montgomerie & Martin 1992) and thus are more difficult to detect. Even if differences in body size between sexes are not negligible in this species, they are probably not large enough and we did not detect any strong effect of sex on either survival or transience probabilities in Audouin's gulls. Surprisingly, both sexes showed a decreasing trend in survival over time. This may be due to density-dependent effects or to environmental factors such as the appearance of carnivores in the colony in the last decade (Tavecchia *et al.* 2007; Almaraz & Oro 2011). Carnivores may cause a decrease in survival through predation, but may also promote the emigration of established breeders, thereby triggering dispersal to other

colonies (Forbes & Kaiser 1994; Oro, Pradel & Lebreton 1999; Almaraz & Oro 2011). This possibility is also supported by the transient analysis, as the probability of transience after recruitment increased over the years.

In agreement with previous studies (Oro, Pradel & Lebreton 1999; Tavecchia *et al.* 2007), the probability of transience clearly depends on the age at recruitment. If an individual was first seen at the colony at 3 or 4 years, the commonest recruitment age (Oro & Pradel 1999, 2000), the probability of its returning to the colony later was very high (close to 1) and in this case did not change over time; however, the probability of transience after recruitment increased with age and over time. Results thus suggest that young breeders experiencing a carnivore presence in the colony that were able to survive were more reluctant (or less able) than older birds to disperse to safer breeding patches. Transients of older ages coming to breed at later ages in the Ebro delta had either bred before at another colony or were individuals that were less prone to breed (see also Oro, Pradel & Lebreton 1999; Tavecchia *et al.* 2007; Péron, Lebreton & Crochet 2010).

Conclusions

The proposed multi-event capture–recapture modelling demonstrates that the use of uncertain field observations should not be ruled out and can actually be very useful. In particular, our example of using behavioural observations to determine the sex of individuals as a means of analysing sex differences in demographic parameters and state transition parameters is shown to be feasible. This approach could be also useful for applied ecologists for assessing the reliability of their criteria for sexing animals in the field, thereby optimizing field protocols, and for exploring the potential sex differences in key demographic parameters in species where sex may be difficult to ascertain. The increase in power resulting from applying our approach should allow researchers to use most of the information gathered during fieldwork, even that with an associated degree of uncertainty.

Acknowledgements

We would like to thank all the people who have helped with the fieldwork in the Ebro delta over the years, particularly Albert Bertolero, Julia Piccardo and the technical staff and volunteers at the Ebro Delta Natural Park. The Associate Editor, Bill Link, and three anonymous reviewers helped to generate an improved version of the manuscript. The study was funded by grants from the Spanish Ministry of Science (ref. CGL2006-04325/BOS and CGL2009-08298). Deborah Bonner and Michael Lockwood edited the English.

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Received 4 August 2011; accepted 16 March 2012

Handling Editor: Tim Coulson

Supporting Information

Additional Supporting Information may be found in the online version of this article.

Fig. S1. Recapture probabilities of Audouin's gulls at the Ebro Delta over the study period (1995–2007) from model averaging.

Appendix S1. Multi-event modeling of sex uncertainty.

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