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Costs of reproduction: assessing responses to brood size manipulation on life-history and behavioural traits using multi-state capture-recapture models

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ABSTRACT *Costs of reproduction are fundamental trade-offs shaping the evolution of life histories. There has been much interest, discussion and controversy about the nature and type of reproductive costs. The manipulation of reproductive effort (e.g. brood size manipulation) may alter not only life-history traits such as future adult survival rate and future reproductive effort, but also behavioural decisions affecting recapture/resighting and dispersal probabilities. We argue that many previous studies of the costs of reproduction may have erroneously concluded the existence or non-existence of such costs because of their use of local return rates to assess survival. In this paper, we take advantage of the modern multistate capture-recapture methods to highlight how the accurate assessment of the costs of reproduction requires incorporating not only recapture probability, but also behavioural 'state' variables, for example dispersal status and current reproductive investment. The inclusion of state-dependent decisions can radically alter the conclusions drawn regarding the costs of reproduction on future survival or reproductive investment. We illustrate this point by re-analysing data collected to address the question of the costs of reproduction in the collared flycatcher and the great tit. We discuss in some detail the methodological issues and implications of the analytical techniques.*

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1 Introduction

Trade-offs linking life-history traits constrain their simultaneous evolution, and are therefore fundamental to the understanding of the evolution of life histories (Roff, 1992; Stearns, 1992). Trade-offs arise when two traits are limited by a single resource, so that increasing one trait can only be done at the expense of the other one (Lessels, 1991). Life-history theory predicts a cost of reproduction, that is, a trade-off between current and future reproduction (Williams, 1966; Charnov & Krebs, 1974; Reznick, 1985). An increase in current reproductive effort might affect the parents' future reproduction (i) by lowering their future survival, hence lowering the probability of future reproduction (e.g. Nur, 1984, 1988, but see Pettifor, 1993), and/or (ii) by lowering their future fecundity or probability of reproducing successfully (e.g. Slagsvold, 1984; Lessels, 1986). The experimental testing of the costs of reproduction has often used manipulations of the number of eggs or young that parents are made to rear. This procedure has been suggested to provide an *a priori* reliable means of determining these costs (Lessels, 1991; Roff, 1992). Until now, such experimental tests have focused exclusively on survival and reproductive traits of parents and offspring (see reviews in Reznick, 1985; Nur, 1990; Lessels, 1991; Roff, 1992; Stearns, 1992).

1.1 Costs of reproduction on future adult survival: recapture/resighting and dispersal probability

Most field studies that investigated costs of reproduction used return rates, i.e. the proportion of individuals present in year t and returning in year $t+1$, as estimates of survival rates (Clobert, 1995; Martin *et al.*, 1995, but see Yoccoz *et al.*, this issue). However, return rates depend on (i) the probability of surviving, (ii) the probability of returning to the study area if alive, and (iii) the probability of being recaptured/resighted if alive and present in the study area (Brownie *et al.*, 1993; Nichols & Kendall, 1995). In many studies, as the recapture probability is not equal to one, return rates will provide biased estimates of survival probability (Lebreton *et al.*, 1992, 1993; Clobert, 1995). The potential consequences of this bias have been discussed previously (Martin *et al.*, 1995), and it has recurrently been advocated that studies attempting to estimate survival probabilities should also estimate recapture/resighting probabilities (Martin *et al.*, 1995). Even when the estimation of exact survival rate is not required (e.g. in comparative analyses, see Martin *et al.*, 1995), a change in return rate may be due to a change in either survival or various underlying behavioural processes (Clobert, 1995).

Differences in return rates among individuals can indeed reflect mere variation in behavioural decisions influencing recapture probability (e.g. 'trap dependence' effect—Pradel, 1993; or decisions to skip breeding, when recapture/resighting is linked to breeding status; see also Viallefont *et al.*, 1995). Moreover, studies are often based on estimates of local survival, not distinguishing between mortality and dispersal (Clobert & Lebreton, 1991; Nichols & Kendall, 1995; Spendelow *et al.*, 1995). Differences in local survival rates among individuals can reflect mere variation in dispersal probability (Högstedt, 1981; Boulinier *et al.*, this issue). The costs of reproduction might be expressed not only in life-history traits, but also in behavioural traits such as the likelihood of breeding or dispersing. Until now, such behavioural consequences of clutch/brood size manipulations have rarely been investigated (but see Viallefont *et al.*, 1995).

1.2 Costs of reproduction in future reproductive investment: information on environmental suitability

Individuals of many species have been shown to modify their clutch/litter size according to the number of young they can raise (Individual Optimization Hypothesis—Perrins & Moss, 1975; Pettifor *et al.*, 1988; Pettifor *et al.*, 2001). Individuals thus adjust their clutch/litter size to an estimate of environmental suitability or parental care ability at the time of young rearing (Högstedt, 1980, 1981; Slagsvold, 1984). Clutch/brood size manipulations may produce a mismatch between the number of young being reared and environmental/parental conditions, and may thus induce a recalibration of such an adjustment rule (Lessels, 1991). This mechanism points out that changes in future fecundity in response to clutch/brood size manipulation are likely to depend on the information gathered by individuals prior to the manipulation, and on how this information is modified by the manipulation. Variation in clutch/litter size may be partly due to individual variation in information on environmental suitability in varying environments (Shettleworth *et al.*, 1988). This information depends on individual's previous experience in the current breeding habitat (Massot *et al.*, 1994; Pärt, 1995), which may in turn depend on dispersal status. Under the Individual Optimization Hypothesis, current reproductive effort before manipulation is also expected to reflect individual information. As a consequence, studies attempting to investigate costs of reproduction on future fecundity should account for individual variables, such as dispersal status or current reproductive effort, which are likely to influence the decision to produce a given clutch/litter size the next year.

1.3 Reassessment of two experimental case studies of costs of reproduction

Two previous experimental studies have investigated potential life-history trade-offs revealing costs of reproduction in the collared flycatcher *Ficedula albicollis* (Gustafsson & Sutherland, 1988) and the great tit *Parus major* (Pettifor *et al.*, 1988). However, neither took into account recapture/resighting and dispersal probabilities, nor included individual variables, as discussed above. In this study, we used multi-state capture-recapture models (Brownie *et al.*, 1993; Nichols *et al.*, 1994; Nichols & Kendall, 1995) to address this issue and attempt to reassess costs of reproduction in these species. We focus on possible changes in four different life-history and behavioural traits following manipulation of current reproductive effort: (i) survival rate; (ii) capture probability; (iii) future reproductive effort; (iv) dispersal rate (in the collared flycatcher only). We concentrate here on the methodological aspects of our analyses. In particular, we show how the inclusion of a behavioural variable (dispersal) can modify the interpretation of evidence for a cost of reproduction, even when appropriate statistical techniques have apparently been employed.

2 Estimating costs of reproduction using multi-state capture-recapture models: methods

2.1 The collared flycatcher study: study site and species

The collared flycatcher is a small, hole-nesting migratory passerine bird breeding in Europe. The data used in this work were collected during a long-term study of a population of collared flycatchers carried out on the Southern part of Gotland,

Sweden (57°10′N, 18°20′E), 1983-1996, in 13 different discrete woodlands (see Pärt & Gustafsson, 1989). The study design allows the detection of individual movements between woodlands, and thus the estimation of dispersal probabilities. Collared flycatchers lay only one clutch per year, and the modal clutch size is six eggs, but ranges from four to eight (very rarely nine). Each year laying date, clutch size, hatching date and number of fledglings were monitored in all nests in boxes throughout the season. All adults caught and fledglings were ringed with individually numbered rings. Adults were trapped and identified while breeding, which implies that adults were caught only when successfully breeding. The collared flycatcher is a facultatively polygynous species, and males are sometimes very difficult to trap at their secondary nests (Gustafsson, 1989). Polygyny is thus a major reason for failure to capture some of the males. More details on the study site and breeding ecology of the collared flycatcher can be found in Gustafsson (1989) and Pärt & Gustafsson (1989).

2.2 Manipulations of clutch/brood size, experimental groups, capture histories and state variables

Clutch/brood size manipulations were performed during three different periods: 1983 to 1985, 1988 to 1990, and 1992 to 1994. Because the collared flycatcher is short-lived, individuals manipulated in these three different periods were in large part different (4.1% of males captured in period 1983-1985 were found again in 1988-1990, and 11.9% from period 1988-1990 in 1992-1994; these percentages were 3.2% and 9.0% respectively for females). Therefore, the three periods can be considered as three quasi-independent replicates of the experiment. Clutches with the same laying/hatching date were randomly treated in pairs, and one or two eggs/young were moved from one nest to the other. Birds were thus randomly assigned to one experimental group: (i) increased or (ii) decreased clutch/brood size, or to the control group (no change in clutch/brood size).

Some individuals have been manipulated several times within each experimental period. When the experimental treatment they received changed between years, or when their clutch/brood size was manipulated only on their second or third capture in the period, their capture-recapture history was cut into two (occasionally three) histories in order to account for the responses to different treatments. The first history included the recapture history until the second experimental manipulation was performed (or the first after a control treatment), and the second history included the history from the second manipulation onwards (or the first after a control treatment). The individual was removed at the end of the first history as if it were not released again, i.e. lost on capture, and the second history was assigned to the new corresponding experimental group. This procedure implicitly assumes that memory effects can be neglected. We chose this approach instead of eliminating these individuals from the analysis in an attempt to keep the highest sample size possible. The total number of capture-recapture histories obtained for the analyses varied from 587 to 918, depending on sex and study period. Capture-recapture histories were constructed over periods of five years, beginning on the first year of each experimental period (1983, 1988 and 1992 respectively). Only individuals that had been caught at least once during one of the three experimental years were included.

In our multi-state histories, we considered two possible state variables: (i) natural clutch size (before manipulation when performed), and (ii) dispersal status. In the

case of natural clutch size, grouping of individuals was necessary to render the analysis tractable (Clobert, 1995). Adult birds were thus assigned to one of three clutch size states as follows: *state 1:* clutches of less than 6 eggs (small clutch size); *state 2:* clutches of 6 eggs (medium clutch size); *state 3:* clutches of more than 6 eggs (large clutch size). In the case of dispersal status, the state variable had two modalities: resident or disperser. A breeding adult was considered as a disperser when (i) it was unringed when caught, or, if ringed, (ii) it had been caught breeding in another woodland on its last capture as a breeder (for two-year old or older individuals) or had been ringed as a chick in another woodland (for one-year old individuals, and older individuals that had not been caught as breeders previously). Any breeding bird caught in its natal woodland, or that had been caught breeding in the same woodland on its last capture occasion was considered as a resident.

For each sex, period, and state variable considered, one set of three demographic parameters (i.e. one survival rate, one recapture rate and one set of transition rates) was modelled, thus giving a total of 3 parameters × 2 sexes × 3 periods × 2 state variables = 36 different parameters investigated.

2.3 The great tit study

A similar experimental approach was used to investigate costs of reproduction in the great tit, a non-migratory species whose breeding biology is similar to that of the collared flycatcher. The great tit data were collected during a long-term study in Wytham Wood, near Oxford (51°46′N, 1°19′W). The study site and general methods associated with this study are given in Perrins (1965, 1979), with specific details on the brood size manipulations in Pettifor *et al.* (2001). Brood size was manipulated in the years 1959-1964 and 1977-1980, with, in most cases, three or four young being removed from, or added to, randomly chosen experimental nests, usually on or just after the day of hatching. The same procedures as described for the flycatcher were applied to the great tit data, except for the assignment of natural clutch size classes. Clutch size is more variable among years and individuals in the great tit than in the flycatcher, the median being either 8 or 9 eggs, but with a range from 2 to 17. Adult birds were therefore assigned to one of three clutch size states as follows: *state 1*: clutches smaller than the median clutch size for the year by two or more eggs; *state 2*: clutches equal in size to the median clutch size ± one egg; *state 3*: clutches larger than the median clutch size by two or more eggs. Capture-recapture histories were constructed in the same way as in the collared flycatcher over the two periods of experimental brood size manipulations, plus a further two years following the last year of manipulation (i.e. 1959-1966 and 1977-1982). Individuals that had been manipulated in more than one year were treated as above. Males were not captured as breeding adults in the first period, so that only females were included in the analyses for this period. The number of capture-recapture histories obtained for analyses varied here from 498 to 525. The total number of survival, recapture and transition parameters modelled for the great tit was 9.

2.4 Statistical methods, data overdispersion and model selection procedure

Males and females were considered in separate analyses. Indeed, sex-specific dispersal patterns have previously been suggested to result from different behavioural mechanisms between sexes in these species (Pärt & Gustafsson, 1989; Doligez

et al., 1999). Furthermore, different reproductive costs may be expected between males and females, due to their different investment in various reproductive activities (incubation and brooding by females alone; incubation feeding by males; differential young feeding and nest defence by both sexes—Perrins, 1979; Sheldon *et al.*, 1997; Michl *et al.*, 2000; see also Nichols *et al.*, 1994).

Multi-state capture-recapture models (Brownie *et al.*, 1993; Nichols & Kendall, 1995) were used to test the effect of experimental clutch/brood size manipulations on four different traits: (i) survival rate; (ii) capture probability; (iii) future reproductive investment (measured by future clutch size); and (iv) dispersal probability. This method allows precise modelling of the variation in the above parameters according to different relevant factors, and, in particular, permits estimation of state-specific survival and recapture probabilities, and transition probabilities between states. The most general model included (i) time-; (ii) experimental group-; (iii) 'pseudo-age'- and (iv) state-specific survival, capture and transition probabilities. The 'pseudo-age' effect was included to investigate and separate possible short-term and long-term effects of clutch/brood size manipulations (e.g. Clutton-Brock *et al.*, 1982; Gustafsson & Pärt, 1990; McCleery *et al.*, 1996). We considered two 'age' classes: one year after the manipulation versus two years or more. Model notation has been extended from the notation defined in Nichols et al. (1994). $S^{s}_{t,a}(g)$ (survival probability) is the probability that a bird of experimental group g and age class a in state s at time $t-1$ survives until time t. $P^{s}_{t,a}(g)$ (recapture probability) is the probability that a bird of group g and age class a is recaptured at time t in state s, given that it is alive and present at time t. $T^{sr}_{t,a}(g)$ (transition probability) is the probability that a bird of group g and age class a in state s at time $t-1$ is in state r at time t given that the individual has survived from year $t-1$ to year t. We used MARK software (White & Burnham, 1999) to compute models' deviance and parameters estimates.

It was not possible to include in a single analysis the two combined state variables (natural clutch size and dispersal status) given the number of parameters required by such a model: with dispersal status (two possible states), the number of transition parameters to be estimated was two. With natural clutch size (three possible states), this number was six. In a model combining both states, the number of transition parameters would increase up to 30. We thus performed two series of analyses: (i) using natural clutch size as the state variable, we first investigated the consequences of clutch/brood size manipulation in terms of survival rate, capture probability and future reproductive effort (transitions between natural clutch size classes); (ii) in a second step (in the collared flycatcher only), using dispersal status as the state variable, we investigated the consequences of manipulation on dispersal probability (transitions between disperser and resident status) instead of future reproductive effort.

Goodness-of-fit (GOF) tests are not available in MARK for multi-state capture-recapture models yet. We attempted to check for data overdispersion by computing GOF tests for the corresponding uni-state data sets (Lebreton *et al.*, 1992; Anderson *et al.*, 1993). We computed TESTS 3 and 2 of the RELEASE option of program MARK (Lebreton *et al.*, 1992), and ran the bootstrap procedure implemented in MARK (White & Burnham, 1999), for the most general model for uni-state data sets, i.e. including time, group and 'pseudo-age' effects. As the bootstrap procedure cannot handle losses on capture, the extra capture-recapture histories computed when individuals had been manipulated several times (see above) were eliminated. Model selection was based on the Akaike's Information Criteria

corrected for effective sample size (AIC_c—Lebreton *et al.*, 1992; Anderson & Burnham, 1994; Burnham *et al.*, 1995; Cooch & White, 2000); the models whose AIC_c value differed by less than two units from the lowest AIC_c model were those selected.

Four different effects were investigated (see above). Thus, the total number of different possible models including only main effects and interactions on survival, capture and transition probabilities (but no additive effects) was 15^3 for each sex, experimental period and state variable considered. Therefore, it was obviously not possible to compute deviance and AIC_c for all models. The model selection procedure adopted was the following. We first checked whether the time effect (the effect of least interest here) could be eliminated by computing deviances and comparing AIC_cs of the eight most general models with or without a time effect (in interaction with the three other factors) on survival, capture and transition parameters. When all those time effects that could be eliminated had been removed, model selection was continued with this simplified model as the reference model. Simplified models of survival probability were investigated first, then capture probability while keeping the simplest model for survival probability, and finally transition probabilities while keeping the simplest models for both survival and capture probabilities. To test the robustness of this selection procedure, we compared AIC_cs of the final selected model(s) with those of models in which some of the eliminated effects were re-introduced on survival and capture probabilities, while keeping the simplest model for transition probabilities. In particular, when selected models differed between periods for the same sex, we computed AIC_cs of the models selected in one period for the other periods (if not done previously). However, we are aware of the weakness of this model selection procedure, which does not allow absolute confidence that the best possible models have been selected. We cannot rule out that some models not investigated here might have smaller AIC_cs than the selected ones. For this reason, we focus here on general results. We did not compute any additive models for the reason given above (keeping the number of possible models to a tractable level). After identifying one or more 'best' models, models with new constraints were built when the treatment effect was retained, to test specific *a posteriori* hypotheses about which experimental groups differed from each other.

3 Results

3.1 Validation of model selection procedures

No overdispersion was observed in any of the uni-state data sets analysed (Table 1). Therefore, the model selection based on AIC_c values seemed valuable (Anderson *et al.*, 1993; Anderson & Burnham, 1994; Burnham *et al.*, 1995). An example of the model selection procedure described above is given in Table 2. The time effect could be eliminated in all cases following this procedure. When the state variable was natural clutch size, some of the models with time effects did not converge due to insufficient data in view of the large number of parameters; their deviance may thus not be reliable. However, time effects could always be removed when convergence was attained. Therefore, we are confident that time effects did not strongly influence survival, capture or transition probabilities. Very often we could not discriminate between several 'best' models (whose AIC_cs differed by less than two units).

TABLE 1. Goodness-of-fit tests for the flycatcher data sets. (a) Results of the RELEASE tests 3 and 2 (χ^2 values and associated probabilities); (b) results of the bootstrap procedure implemented in MARK (probability of obtaining the observed deviance of the model—$p > 0.05$ indicates no overdispersion of data—and observed $\hat{c}$ values). The number of simulations was 500 in each case

(a)

Test	Period	Males	Females
Test 3	1983-1987	$\chi^2_{12} = 9.399$, $p = 0.67$	$\chi^2_{12} = 7.740$, $p = 0.81$
	1988-1992	$\chi^2_{8} = 3.763$, $p = 0.88$	$\chi^2_{11} = 4.552$, $p = 0.95$
	1992-1996	$\chi^2_{12} = 7.241$, $p = 0.84$	$\chi^2_{10} = 2.323$, $p = 0.99$
Test 2	1983-1987	$\chi^2_{6} = 3.852$, $p = 0.70$	$\chi^2_{5} = 3.343$, $p = 0.65$
	1988-1992	$\chi^2_{4} = 1.547$, $p = 0.82$	$\chi^2_{5} = 7.396$, $p = 0.19$
	1992-1996	$\chi^2_{6} = 1.518$, $p = 0.96$	$\chi^2_{2} = 0.000$, $p = 1.00$
Tests 3 and 2 combined	1983-1987	$\chi^2_{18} = 13.251$, $p = 0.78$	$\chi^2_{17} = 11.083$, $p = 0.85$
	1988-1992	$\chi^2_{12} = 5.310$, $p = 0.95$	$\chi^2_{16} = 11.947$, $p = 0.75$
	1992-1996	$\chi^2_{18} = 8.759$, $p = 0.97$	$\chi^2_{12} = 2.323$, $p = 0.99$

(b)

Period	Males	Females
1983-1987	$p = 0.14$, $\hat{c} = 1.229$	$p = 0.11$, $\hat{c} = 1.118$
1988-1992	$p = 0.16$, $\hat{c} = 1.344$	$p = 0.12$, $\hat{c} = 1.336$
1992-1996	$p = 0.95$, $\hat{c} = 0.526$	$p = 0.26$, $\hat{c} = 0.726$

3.2 General results: evidence for a manipulation effect but not for a cost of reproduction

A total of 45 survival, capture and transition parameters were modelled across both species (36 for the flycatcher and 9 for the great tit—see Methods). An effect of experimental clutch/brood size manipulation could be found in 13 out of these 45 parameters, although the alternative model without manipulation effect on the parameter considered was also selected in 8 cases out of 13. *A posteriori* tests showed that, in 7 cases out of 13, the parameters differed between manipulated and non-manipulated individuals, but not between individuals of the decreased and increased groups. 'Decreased' and 'increased' individuals differed in 7 cases (the capture probability of females flycatchers in the first period belongs to both categories; it did not differ between decreased and increased females when they laid small clutches, but differed when they laid medium or large clutches). In only one of these seven latter cases did decreased and increased individuals differ as predicted by a cost of reproduction: flycatcher survival rate in the third period was smaller for females of the increased group, and higher for females of the decreased group, compared with the control group (the state variable being clutch size) (Fig. 1(a)). However, this pattern seemed to be due to differential dispersal (see below).

In summary, the results do not provide evidence for the existence of costs of reproduction on survival or future reproductive investment. When the brood size manipulation (i.e. group) effect was retained in a selected model, (i) one or several alternative models with no group effect were often selected at the same time; and (ii) except in one case, we did not observe the patterns predicted under costs of reproduction (i.e. reduced future adult survival rate and/or future reproductive investment for individuals from the increased group compared with the control group, and vice-versa for individuals from the decreased group). Neither did we find a clear effect of clutch/brood size manipulation on capture and dispersal

TABLE 2. An example of the model selection procedure for collared flycatcher females in the period 1983–1987. The state variable is the dispersal status. In each of the sub-tables, models are ranked by increasing value of AIC_c, and the bold lines indicate the set of 'best' models (lowest AIC_c values, with difference in AIC_cs smaller than 2). At the end of each selection step, the simplest model was retained as the starting model for simplification in the next step

FIRST STEP: CHECKING FOR TIME EFFECTS

Model	Deviance	Nb parameters	AIC_c
$\boldsymbol{S^s_a(g), P^s_a(g), T^{sr}_a(g)}$	**2135.917**	**36**	**2210.46**
$S^s_a(g), P^s_{t,a}(g), T^{sr}_a(g)$	2097.626	66	2238.31
$S^s_a(g), P^s_a(g), T^{sr}_{t,a}(g)$	2104.752	66	2245.43
$S^s_{t,a}(g), P^s_a(g), T^{sr}_a(g)$	2113.969	66	2254.65
$S^s_{t,a}(g), P^s_{t,a}(g), T^{sr}_a(g)$	2075.407	84	2257.67
$S^s_a(g), P^s_{t,a}(g), T^{sr}_{t,a}(g)$	2077.936	96	2288.77
$S^s_{t,a}(g), P^s_a(g), T^{sr}_{t,a}(g)$	2082.684	96	2293.52
$S^s_{t,a}(g), P^s_{t,a}(g), T^s_{t,a}(g)$	2063.238	114	2318.24

SECOND STEP: SIMPLIFYING MODELS OF SURVIVAL RATE

Model	Deviance	Nb parameters	AIC_c
$\boldsymbol{S, P^s_a(g), T^{sr}_a(g)}$	**2148.062**	**25**	**2199.29**
$\boldsymbol{S^s, P^s_a(g), T^{sr}_a(g)}$	**2147.762**	**26**	**2201.08**
$\boldsymbol{S_a, P^s_a(g), T^{sr}_a(g)}$	**2147.892**	**26**	**2201.21**
$S(g), P^s_a(g), T^{sr}_a(g)$	2146.460	27	2201.89
$S^s_a, P^s_a(g), T^{sr}_a(g)$	2145.683	28	2203.22
$S_a(g), P^s_a(g), T^{sr}_a(g)$	2142.063	30	2203.82
$S^s(g), P^s_a(g), T^{sr}_a(g)$	2142.390	30	2204.16
$S^s_a(g), P^s_a(g), T^{sr}_a(g)$	2135.917	36	2210.46

THIRD STEP: SIMPLIFYING MODELS OF RECAPTURE PROBABILITY

Model	Deviance	Nb parameters	AIC_c
$\boldsymbol{S, P, T^{sr}_a(g)}$	**2152.798**	**14**	**2181.19**
$\boldsymbol{S, P^s, T^{sr}_a(g)}$	**2152.579**	**15**	**2183.03**
$\boldsymbol{S, P_a, T^{sr}_a(g)}$	**2152.598**	**15**	**2183.05**
$S, P(g), T^{sr}_a(g)$	2152.154	16	2184.66
$S, P^s_a, T^{sr}_a(g)$	2152.101	17	2186.67
$S, P_a(g), T^{sr}_a(g)$	2149.968	19	2188.68
$S, P^s(g), T^{sr}_a(g)$	2150.686	19	2189.40
$S, P^s_a(g), T^{sr}_a(g)$	2148.062	25	2199.29

FOURTH STEP: SIMPLIFYING MODELS OF TRANSITION PROBABILITY

Model	Deviance	Nb parameters	AIC_c
$\boldsymbol{S, P, T^{sr}_a}$	**2165.423**	**6**	**2177.50**
$\boldsymbol{S, P, T^{sr}(g)}$	**2162.447**	**8**	**2178.58**
S, P, T^{sr}	2172.505	4	2180.54
$S, P, T^{sr}_a(g)$	2152.798	14	2181.19
$S, P, T_a(g)$	2262.766	8	2278.90
S, P, T_a	2271.178	4	2279.22
$S, P, T(g)$	2285.983	5	2296.04
S, P, T	2294.811	3	2300.83

TABLE 3.—(*Continued*)

FIFTH STEP: CHECKING THE SELECTED MODELS AGAINST OTHER MODELS BY REINJECTING SIMPLE EFFECTS ELIMINATED DURING PREVIOUS STEPS OF MODEL SELECTION

Model	Deviance	Nb parameters	AIC_c
$\boldsymbol{S, P, T_a^{sr}}$	**2165.423**	**6**	**2177.50**
$\boldsymbol{S, P, T^{sr}(g)}$	**2162.447**	**8**	**2178.58**
$\boldsymbol{S, P^s, T_a^{sr}}$	**2164.916**	**7**	**2179.02**
$\boldsymbol{S, P_a, T_a^{sr}}$	**2165.222**	**7**	**2179.33**
$\boldsymbol{S^s, P^s, T_a^{sr}}$	**2165.276**	**7**	**2179.38**
$\boldsymbol{S_a, P^s, T_a^{sr}}$	**2165.365**	**7**	**2179.47**
$S, P_a, T^{sr}(g)$	2162.247	9	2180.41
$S^s, P, T^{sr}(g)$	2162.320	9	2180.49
$S_a, P, T^{sr}(g)$	2162.389	9	2180.56
$S(g), P, T_a^{sr}$	2164.429	8	2180.56
$S, P^s, T^{sr}(g)$	2162.447	9	2180.61
S, P, T^{sr}	2172.505	4	2180.54
S^s, P^s, T_a^{sr}	2164.621	8	2180.76
$S, P(g), T_a^{sr}$	2164.779	8	2180.91
S_a, P^s, T_a^{sr}	2164.860	8	2180.99
S_a, P_a, T_a^{sr}	2164.884	8	2181.02
S^s, P_a, T_a^{sr}	2164.968	8	2181.10
$S_a, P_a, T^{sr}(g)$	2161.909	10	2182.11
$S^s, P_a, T^{sr}(g)$	2162.023	10	2182.23
$S^s, P^s, T^{sr}(g)$	2162.299	10	2182.50
$S_a, P^s, T^{sr}(g)$	2162.386	10	2182.59
S, P^s, T^{sr}	2172.499	5	2182.55
$S(g), P, T^{sr}$	2171.511	6	2183.59
$S, P(g), T^{sr}$	2171.860	6	2183.94
S^s, P^s, T^{sr}	2172.379	6	2184.46
$S(g), P^s, T^{sr}$	2171.508	7	2185.61
$S^s, P(g), T^{sr}$	2171.674	7	2185.78
$S(g), P(g), T^{sr}$	2170.588	8	2186.72
S, P^s, T	2200.177	4	2208.22
$S, P^s, T(g)$	2196.910	6	2208.99
S^s, P, T	2294.634	4	2302.67

probabilities. Rather, the results suggest an effect of the manipulation itself, since, in many cases, birds from the increased and decreased groups did not differ, but differed from birds of the control group. The results also illustrate temporal variability in responses to factors affecting life-history and behavioural traits, which is a classical result in previous studies (Nur, 1988). Indeed, the selected models differed according to the period considered (see also Pettifor *et al.*, 2001).

3.3 The importance of including behavioural variables: the case of dispersal probability in the collared flycatcher

When using clutch size as the state variable, female flycatcher survival in the third period was lower in the increased group, and higher in the decreased group, compared with the control group (Fig. 1(a)). This was the only case where the obtained pattern of parameter variation matched the one predicted under a cost of reproduction. The model with no group effect (constant survival) was, however, also selected. When considering dispersal status as the state variable, for the same period, the difference in survival rate for females of different groups disappeared.

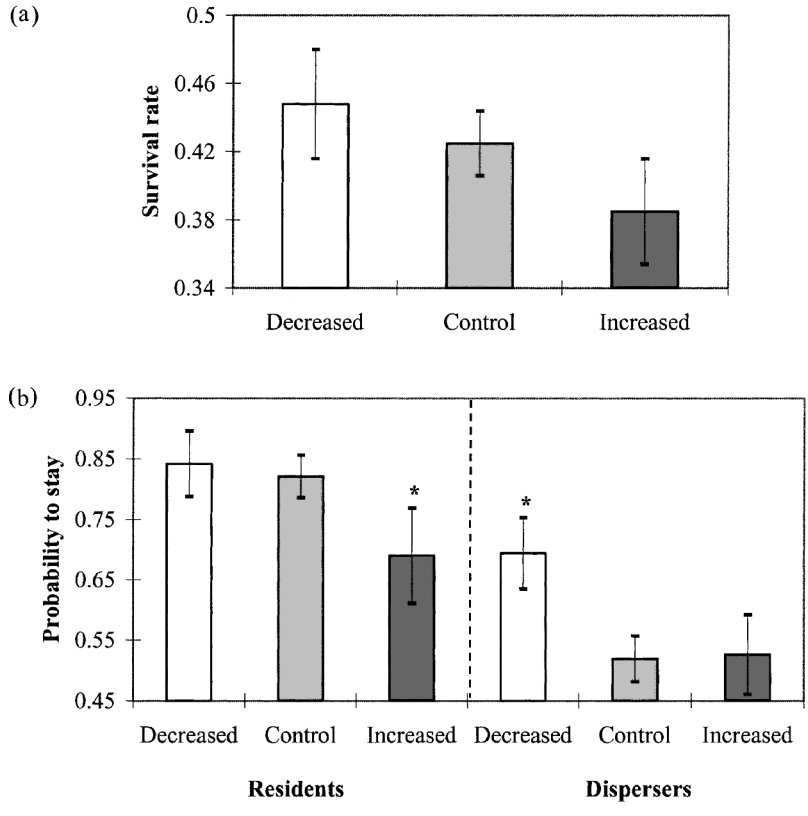

FIG. 1. (a) Survival probabilities (± 1 s.e.) of collared flycatcher females for the period 1992-1996, with clutch size class as the state variable, according to experimental treatment: increased clutch/brood size (increased); decreased clutch/brood size (decreased); control (see text). $N = 895$. *A posteriori* models constraining parameters, constructed to determine which experimental groups differed, showed that female survival rate for the decreased group was higher than female survival rate for the increased group, while female survival rate for the control group did not differ from the two other groups. However, the alternative model with no group effect on survival was also selected in this case (AIC_cs of the models with and without a group effect differed by less than two units). (b) Probability for collared flycatcher females to stay in their breeding area the following year (± 1 s.e.), for the same period (1992-1996), according to experimental treatment (same as in part (a)), and previous dispersal status. The state variable here was dispersal status. Models constructed *a posteriori* showed that the probability of staying was lower in the increased group for resident females, and higher in the decreased group for dispersing females (as indicated by the asterisks); the two other probabilities did not differ between each other in either residents or dispersers.

In this case, female dispersal probability differed according to previous dispersal status and group (Fig. 1(b)), although the alternative model with no group effect (dispersal status alone) was also selected. The previously observed pattern in survival could, in fact, be explained by differential dispersal probability between females of different groups. Resident females whose brood had been enlarged were more likely to leave their breeding patch than other females, thus more likely to disperse out of the study area and less likely to be caught again. As a result, females from the increased group had, on average, a lower local, apparent survival rate (Fig. 1(a)), and capture probability. Similarly, dispersing females whose brood size had been decreased were more likely to become resident; thus, females from the decreased group had a higher average local, apparent survival rate.

4 Discussion: current limitations of the use of multi-state capture-recapture models

Differences in survival, capture and transition parameters among experimental groups were often retained in our study, but these differences almost never supported costs of reproduction. The biological implications of our results will be discussed elsewhere. We focus here on the methodological issues and implications of our study, and on some aspects of the use of multi-state capture-recapture models in evolutionary biology in general. Our analyses were constrained by three types of limitation: (i) technical and practical limitations, including data limitation; (ii) limitations of modelling tools; and (iii) limitations of theoretical predictions. Below, we discuss the first two issues, emphasizing the need for future work aimed at developing the use of multi-state capture-recapture models for the study of evolutionary questions to address these issues.

4.1 Technical limitations

4.1.1 Number of parameters to be estimated in complex models. The use of multi-state capture-recapture models permits powerful testing of various predictions about behaviour and physiology (Nichols *et al.*, 1994; Clobert, 1995; Nichols & Kendall, 1995), but such models use a large number of parameters. In particular, the number of transition parameters rapidly 'explodes' with the number of states: for n states, the number of possible transitions between states to be modelled is $n(n-1)$, i.e. is a function of n^2. Multistate models thus require (i) computation power, and (ii) large data sets. Computer facilities currently available no longer limit calculations. Conversely, the number of individuals in each possible cell describing transitions between states has to remain sufficiently large to allow estimation of transition probabilities. Thus, multi-state models involving a large number of states (e.g. when studying movement rates between sites) require much larger data sets than 'classical' capture-recapture models. It will often be necessary to adopt strategies to limit the number of different states, for instance grouping data into classes as we did here with clutch size, so as to make analyses tractable (Clobert, 1995; Nichols & Kendall, 1995). However, such limitation might also constrain the biological hypotheses that can be investigated.

In our case, the two state variables considered—natural clutch size and dispersal status—could not be included in a single analysis. When three different states were possible (clutch size as the state variable), convergence was already questionable or non-existent for some of the most complicated models (in particular those with time effects), and estimates of transition probabilities were in some cases aberrant (e.g. the sum of transition probabilities from one state to all others was greater than one). It was not clear whether some of these models should be kept in the analysis or removed, and on which criteria to base such a decision. However, we believe that the number of states that were considered here to address our biological questions was not unreasonable given our data sets.

When addressing the question of dispersal, using site as the state variable would allow us to account for variability between sites in dispersal rate (see for example Morris, 1987). However, this procedure requires far too many states for the analysis to be tractable as soon as more than two sites are considered (for example, here, flycatchers were caught in 13 different sites). Using site characteristics (e.g. size, or breeding pairs density) as individual covariates (Skalski *et al.*, 1993) is another

way to tackle the question of site variability, but requires dynamic covariates since individuals may change sites (see below).

Future developments in capture-recapture theory may inflate this problem. For example, incorporating long-term memory effects in models can only increase the need for larger data sets. The Bayesian approach may, in turn, be a way to increase analytical power without demanding more parameters, owing to the use of prior information (see Dupuis, this issue). The current need for such large data sets both justifies the existing efforts to sample populations in the field and calls for even more effort in the future.

4.1.2 Number of possible models to be 'ideally' run and model selection strategy. The influence of four factors on survival, capture and transition parameters was tested here. Well-designed experiments usually allow the number of factors under investigation to be limited to a tractable few, but a total of four factors is not uncommon in biological field studies. As emphasized above, the total number of possible models to be 'ideally' run to determine the best model(s) is also very large even for a limited number of factors (here four), and 'explodes' when the number of factors considered increases. Indeed, in multi-state capture-recapture models, the 'model landscape' to be explored is three-dimensional. Thus, it will often appear necessary to follow specific model selection strategies investigating a restricted subset of models. Future work might prove useful concerning the criteria and strategies to be used to allow efficient but limited model selection procedures.

4.1.3 Current development of software: goodness-of-fit tests. Our approach to test goodness-of-fit was limited to 'uni-state' data sets (i.e. the different states were not considered). Thus, we could only test the absence of heterogeneity among groups for 'global' (i.e. across states) survival and capture probabilities. We did not use $QAIC_c$ for model selection as tests did not reveal significant overdispersion, although (i) the results of the bootstrap GOF procedure were sometimes at the limit of recommended correction, i.e. $p < 0.2$ and/or $\hat{c} > 1.3$, and (ii) the lack of power to detect such overdispersion with TESTS 3 and 2 of RELEASE is well known (Cooch & White, 2000). Without appropriate goodness-of-fit tests for multi-state capture-recapture data, we could not rule out that the data were overdispersed. This could arise for example as a result of group behaviours, in which individuals may change state non-independently from other individuals of their group (e.g. group migration or exploration).

These technical limitations combine with limitations of the capture-recapture modelling tools to prevent the investigation of more specific evolutionary questions.

4.2 Limitations of modelling tools

4.2.1 Temporal pattern of state transition. Current multi-state models assume that the transition from one state to another (such as dispersal movement, decision to breed, decision to lay a given number of eggs) occurs at the end of the time interval considered to calculate survival rate (Brownie *et al.*, 1993; Nichols & Kendall, 1995). This assumption was met here in both biological models: (i) mortality is likely to occur mostly during the winter (non-breeding) season in birds (see Högstedt, 1981), especially in migrating species such as the collared flycatcher, and (ii) capture and assignment to a given state were associated here with breeding activity in both the collared flycatcher and great tit. When capture/resighting is not

linked to the activity for which states have been defined, or when transition may occur at any time in the life-cycle, this assumption is no longer met. Tricky modelling manipulations may then be required. Separating survival and transition between states in multi-state models is needed to relax this constraining assumption, allowing a generalized use of these tools, whatever the recapture/resighting design.

4.2.2 Individual covariates. Given the technical difficulty of investigating all responses to clutch/brood size manipulation considered here in a single analysis (see above), we used a two-step approach. A more general approach to account for both clutch size and dispersal status in the same analysis could have been to analyse separately the capture histories of dispersers and residents at the time when they were first manipulated, with clutch size as the state variable, and compare the models selected for both categories of individuals. This method could probably not have been implemented here because small sample sizes would have prevented efficient model selection. Indeed, some of the complex models did not converge even when grouping all individuals (see above). Dispersal status could also have been included as an individual covariate. However, our results showed that future dispersal probability often depended on previous dispersal status, as well as on age or experimental clutch/brood size manipulation. Both dispersal status and reproductive investment are thus dynamic states, susceptible to change over the course of an individual's lifetime, and could not be considered fixed at the first capture. However, no currently available capture-recapture modelling program allows individual covariates to change through time (i.e. dynamic individual covariates—Clobert, 1995), unless covariate values are known or can be inferred for occasions when individuals are not captured. Therefore, the effect of manipulation on dispersal could not have been accounted for by using dispersal status as a covariate. Neither could we investigate how natural clutch size prior to manipulation influences the effect of manipulation on dispersal probability by using clutch size as an individual covariate. The ability to incorporate dynamic individual covariates in capture-recapture models is badly needed, especially when one addresses questions concerning either behavioural or physiological mechanisms underlying life-history trade-offs.

4.2.3 Memory effects. Further work on multi-state capture-recapture modelling is also needed to include possible memory effects, i.e. the dependence of future life-history and behavioural traits on previous capture-recapture history, or previous experience (e.g. experimental manipulation). Such memory effects have already begun to be incorporated in models accounting for dependence on previous year's factors, i.e. a one-year time step (Brownie *et al.*, 1993; Nichols *et al.*, 1993). While this is likely to be sufficient for short-lived species, investigating life-history patterns and evolution in long-lived species will require modelling memory effects over longer periods (Stearns, 1992). This raises the question of which patterns are to be expected in which conditions and life-cycles, a theoretical issue completely ignored until now.

4.3 Conclusion

With multi-state capture-recapture models, three limits have now been reached: (i) the data limit (i.e. the need for larger data sets to allow powerful analysis with available tools), (ii) the modelling tool limit (i.e. the need to develop tools allowing

specific biological questions to be answered), and (iii) the theoretical limit (i.e. the need for more specific predictions to be tested about which life-history traits we should expect to be affected by costs of reproduction). To improve our understanding of life history evolution, we need to work further in these three major research axes. Further effort should also be made to incorporate these techniques in a wider range of biological studies (both regarding the design of experiments and the analysis of data), many of which still largely ignore the capture-recapture approach (Clobert, 1995; Viallefont *et al.*, 1995).

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