Effect of predation risk, body size, and habitat characteristics on emigration decisions in mallards

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Understanding the processes underlying emigrating behavior is fundamental to better understand animal dispersal. Because of the difficulties involved in carrying out controlled manipulation of the proximate drivers of emigration over large spatial scales, results from laboratory or small field enclosures suitable for small-bodied species remains to be validated in natural habitats. We investigate whether emigration is driven either by intraspecific competition or resulted from hunting-risk avoidance and assessed the effect of phenotypic variation on individual decisions. We made use of a quasi-experimental situation by using hunting recoveries of mallards (*Anas platyrhynchos*) released as ducklings in a fragmented landscape managed for duck hunting. Our results suggest an indirect effect of hunting on emigration. Body size plays a major role in modulating individual emigrating decisions, with small-bodied individuals emigrating more to escape from high levels of predation pressure while larger bodied individuals being more vulnerable to predation. *Key words: Anas platyrhynchos*, dispersal, hunting pressure, multistate recovery models. *[Behav Ecol]*

INTRODUCTION

Dispersal is a keystone process in both population dynamics and evolutionary ecology (Johnson and Gaines 1990; Clobert et al. 2001). Determining the costs and benefits of dispersal is essential to understand its evolutionary causes (Morris 1987) as well as its consequences for spatial population dynamics (Ims and Yoccoz 1997). In the context of both evolutionary and applied ecology, there is a strong need to better understand the proximate and ultimate causes of dispersal in fragmented populations of both threatened and managed species (Kokko and López-Sepulcre 2006).

Emigration, the behavioral decision of departing from the natal or breeding habitats, may be promoted by different ecological processes that rarely operate independently of each other (Clobert et al. 2001). Despite the importance of providing robust quantitative demographic and movement estimates of populations inhabiting fragmented landscapes, few studies have empirically and simultaneously assessed the importance of several ecological drivers of emigration (Hanski 2001).

The main reasons underlying such shortage of studies in vertebrates (but see Blums et al. 2003; Doligez and Clobert 2003) are the logistic difficulties of setting up experimental manipulations (i.e., altering predation pressure, resource abundance, or the intensity of competition) and of marking and following individuals (as a means of estimating their survival and/or reproductive success). The importance of the main drivers of vertebrate emigration over relevant spatial scales and under natural conditions remains poorly investigated (Doncaster et al. 1997; Doligez and Clobert 2003). Moreover, classifying individual movement as dispersal requires to some extent defining either discrete habitat patches or a minimum displacement distance in the field, which often involves arbitrary decisions. Alternatively, ecologists have resorted to experimental manipulations in laboratory or small field enclosures that are mainly suitable for small-bodied species (e.g., Lin and Batzli 2004; Cote and Clobert 2007), but the generality of their findings remains to be validated under natural conditions.

Among the processes known to promote emigration are competition avoidance (be it due to strong social interactions, Ekman et al. 2002, or resource depletion, Matthysen 2005), small size or low quality of the natal habitat (Lin and Batzli 2004), inbreeding avoidance (Lambin 1994; Gandon 1999; Perrin and Mazalov 2000), high prevalence of parasites (reviews in Clobert et al. 2001), body condition (e.g., van der Jeugd 2001; Ekman et al. 2002; Barbraud et al. 2003), or high predation pressure (Doligez and Clobert 2003; Yoder et al. 2004). Andreassen et al. (2002) reviewed the proximate drivers of emigration and identified predation, intraspecific competition, individual characteristics (body size or quality), and habitat characteristics (patch shape, size, and structure) as the main features promoting emigration in vertebrates. In this study, we examined these 4 proximate drivers of emigration by taking advantage of a quasi-experimental situation involving hunting recoveries of mallards (*Anas platyrhynchos*) released for hunting in a naturally fragmented area where body size and the characteristics of the release habitat of each individual were precisely known (see below). Hunting has both a direct (mortality per se) and an indirect (disturbance) effect on the prey population. Nonlethal effects of hunting such as disturbance would thus be perceived as predation risk by ducks (Frid and Dill 2002; see also Cresswell 2008 for a review of nonlethal effects on birds).

Lake area and number of released ducklings provide an indication of relative resource availability and intraspecific competition. In addition, we assess the importance of body size that is commonly invoked in movement decisions, dispersal, and/or survival in Anatidae (e.g., Larsson et al. 1998;

van der Jeugd 2001; Blums et al. 2003). We propose 2 non-mutually exclusive hypotheses of whether emigration is driven by predation risk or intraspecific competition.

HYPOTHESIS AND PREDICTION

Hypothesis 1

If emigrating behavior is induced by intraspecific competition avoidance, emigration rates should increase with high local abundance and decline with increasing lake area (at a given population size). We may expect to find different emigration rates according to the social status of individuals. Larger individuals would perform better in competition for resources and thus have a lower emigration rate than smaller individuals.

Hypothesis 2

When building our hypothesis and predictions in relation to predation risk, we start by recognizing the emigration decision (at large spatial scale) as a patch departure decision (at a feeding patch scale) and follow the general framework of the ecology of fear (sensu Brown and Kotler 2004). If food patches were equivalent in term of foraging costs and differ in term of predation risk, then

(1) it is expected that individuals spend less time in risky habitat than in safer ones.

If emigrating behavior were a response to strong predation risk, emigration rate would increase with hunting pressure.

(2) Individuals with higher energy state or survivor's fitness should spend less time in risky habitats (Brown 1992), whereas individuals with higher marginal value of energy should spend more time in risky habitats.

If (1) is supported, we would expect a positive relation between individual body size and emigration rate.

MATERIALS AND METHODS

Study area and species

The study was conducted between 2002 and 2005 in Brenne (central France, 46°46′N, 01°10′E), a 80 000 ha area entirely devoted to fish farming and duck hunting that is covered by forests, wet meadows, and more than 2000 lakes constituting a patchy network. Mallards comprise at least one-half of the 10 000–20 000 individuals of the 8 duck species wintering in Brenne (counts were done in January, Bourguemestre F, unpublished data), and it is the main game species in this area because about 48 000 individuals are harvested yearly (total bag for France in 1998–1999 was 1.5 million: Mondain-Monval and Girard 2000) during the hunting season (1st September to 31st January). Sustaining high annual harvesting rates of mallards in Brenne is possible because of the release of 30 000–50 000 mallards each summer before the hunting season.

Banding, recoveries, and ecological covariates

We banded 3733 mallards in 32 release lakes between 2002 and 2004 with metal rings from the Museum National d'Histoire Naturelle (Paris). We were able to keep track of recoveries of dead individuals away from Brenne through the French national ringing scheme. We established agreements with hunters associated to the Fédération Départementale des Chasseurs de l'Indre and the Association des Chasseurs de Gibiers d'Eau de l'Indre that allowed us having a particularly high recovery rate (35%; see below) of banded birds over a large area (80 000

Table 1

Number of banded and released mallards recovered or not in Brenne between 2002 and 2004 split by sex and year

	Releases		Recoveries						Not recovered
			2002		2003		2004		
	♂	♀	♂	♀	♂	♀	♂	♀	
2002	891	763	237	271	18	13	10	2	1103
2003	867	813			318	299	20	17	1026
2004	185	214					59	50	290

ha) and to know the precise date and place of death of 1314 ducks recovered by hunters on 125 lakes in Brenne. Unlike other recovery analyses where releases and cumulated recoveries were cumulated at a yearly time step (e.g., Brownie et al. 1985, see also Gauthier and Lebreton 2008), our high recovery rates allowed using the month as the time step in our analyses (Tables 1 and 2). All analyses were conducted at the level of the entire study area rather than at the level of single lakes due to important variation in the cumulative number of ducklings released among lakes (Tables 1 and 2) and because the small number of exchanges between pairs of lakes would prevent model fitting. We gathered data for 5 covariates related to the 2 hypotheses listed above that are likely to explain the observed variation in transition probabilities (see below). These were classified into individual-level (sex, age, and condition at the moment of release) and cohort-level (hunting pressure, size of the release cohort, and area of the release lake) covariates. For each hunting season, the cohort size was defined as the number of mallards released in each lake over the summer.

Body size index
Because juveniles were released at different ages (average = 52.2 days ± 47.7 standard deviation) and they had not attained their asymptotic body size, we did not use the body size index (the residuals of body mass corrected for structural size) previously used in other studies involving adult mallards (e.g., Dufour et al. 1993). Instead, we calculated an "age condition index" as the residuals of the body weight corrected by age (in days) obtained after separately fitting the sex-specific nonlinear regressions estimated by Lokemoen et al. (1990) for mallards. Positive values of this index indicate high-quality individuals that were heavier than average for their age at the moment of release. Because the age condition index could in principle reflect either body size, body condition, or a mixture of both, we aimed to separate the effects of body size and weight on body condition for juvenile mallards. This was done by using a subsample of these juveniles measured again subsequently when having completed growth. An index

Table 2

Summary statistics (mean, standard error, and range) of the covariates used to explain the variation in the state transition probabilities

	Cohort size At each release event	Body size Corrected weight (g)	Hunting pressure Number of hunters per lake per month	Lake area (ha)
Mean ± SE	86.8 ± 14.6	732.9 ± 2.8	27.6 ± 6.4	11.5 ± 2.0
Range	2–528	490–1209	2–120	1.65–45.69

of body size was obtained by using the scores of the first principal component (PC1) estimated from a variance–covariance matrix of 5 morphological variables (tarsus, wing length, tail and bill lengths, and bill height and width). PC1 accounted for 42% of the total variation. Using individual PC1 score as an index of its body size, an index of body condition was obtained by regressing body mass against PC1. Age condition and body condition indices were compared for 28 (13 females and 15 males) released mallards after their recovery by hunters. The age condition index was significantly and positively related with PC1 ($F_{1,11} = 12.53$, $P = 0.004$; adjusted $R^2 = 0.49$ for females and $F_{1,13} = 6.27$; $P = 0.026$; adjusted $R^2 = 0.27$ for males, see Figure 1) but not with the "body condition index" (all $P > 0.5$). We can therefore assume that age condition index reflects the body size of fully grown individuals rather than their body condition.

Hunting pressure estimation

Because hunters pay access fees to single lakes for the entire hunting season at our study site, we considered the cumulative number of hunters present at each lake as a reasonable estimate of the relative hunting pressure among lakes. We also considered the hunting frequency (number of hunting occasions in a month in each lake) as a surrogate of hunting disturbance. The number of hunting occasions differs among lakes because typically all hunters having purchased their access rights to a lake gather at frequencies varying from twice a week to once a month. Information on hunting pressure and frequency was obtained from questionnaires specifically sent to lake owners (corresponding to about 10% of the 4000–4500 hunters per year in Brenne), wherein ducks were both released and recovered at the end of the hunting season. Hunting pressure and frequency data were available for the 32 release lakes and for 57 of the 95 lakes where recoveries took place between September 2002 and January 2004.

Among our 4 covariates, hunting pressure was positively correlated with lake area and cohort size ($r = 0.38$, $P = 0.03$ and $r = 0.45$, $P = 0.01$, respectively; $N = 32$). All other correlations between the 5 covariates were not statistically significant (all $P > 0.26$).

Statistical models

Models without covariates

To our knowledge, no existing general framework allows analyzing multisite recovery data (see Schwarz et al. 1993; Kendall et al. 2006 for modeling approaches involving mixtures of recoveries and recaptures). We therefore formulated a multistate capture–recapture model (Williams et al. 2002) to simultaneously estimate apparent survival (φ), state transition (ψ, in our case, emigration vs. resident), and recovery probabilities (P) of released individuals over space and time. Transition probabilities in this case are a product of survival and movement probabilities. Multistate models can be considered as canonical because all other (uni- or multisites) capture and recovery models can be formulated as special cases depending on the definitions of states and on assumptions made for the recapture/recovery and survival probabilities (Lebreton and Pradel 2002; Gauthier and Lebreton 2008). The goal of this analysis was to investigate the relative importance of different covariates related to our 2 hypotheses on mallard emigration behavior. We defined 3 mutually exclusive states in our model: alive (A), killed at either the release lake (B), or at a different lake (C). Therefore, the transitions $\psi_{A \to B}$ and $\psi_{A \to C}$ denote the monthly recovery rates at either the release site or elsewhere in Brenne and $\psi_{A \to A}$ is by definition the apparent survival probability. As customary in recovery analyses, individuals can only be seen at the moment of release and once they
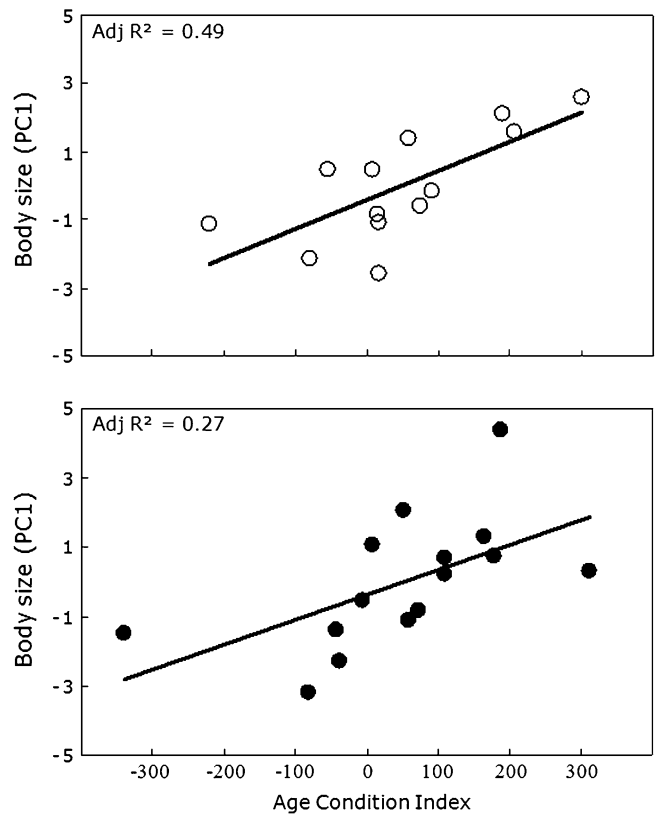
Figure 1
Relationships between body size of ducklings estimated at the time of release (age condition index) and the scores of the first principal component (PC1) obtained from the variance–covariance matrix of 5 morphometric variables measured on fledged individuals recovered during the subsequent hunting season. Females are shown in white and males in black symbols.

are recovered. Based on these state definitions, we fixed the values of those transitions that were either impossible ($\psi_{B \to A} = \psi_{B \to C} = \psi_{C \to B} = \psi_{C \to A} = 0$; $P_A = 0$; $\varphi_B = \varphi_C = 0$) or true by definition ($\varphi_A = 1$) and focused on estimating the remaining parameters. Our multistate model made the customary assumption (Williams et al. 2002) that the allowable state transitions took place at the end of each monthly interval such that departing individuals spent almost all of each time interval at the release lake and were killed on arrival at the lake of destination. Thus, although each monthly transition $\psi_{A \to C}$ actually involves 3 consecutive events (surviving at the release lake, quitting this site, and being killed on arrival at the lake of destination), hereafter we will call and interpret $\psi_{A \to C}$ as an emigration probability and $\psi_{A \to B}$ as probability of remaining on the release site based on the customary assumption of multistate models that state transitions occur toward the end of each monthly time interval.

The statistical analyses of recoveries proceeded in 2 stages. First, we searched for a parsimonious description of recoveries and state transitions (hereafter, the basic model) over time and later incorporated the covariates and their interactions to explain and model the estimated transition rates at the individual level. In seeking the basic model, we built a set of a priori biologically relevant models including combinations of age (juveniles and adults; the latter defined as individuals older than 1 year that survive the first year after release), sex, and time (either constant or including monthly variation both within and between hunting seasons) for each of these 2 parameters. We used the Akaike Information Criterion (AIC)

corrected criterion (AICc for sample size; Burnham and Anderson 1998) to select the model providing the most parsimonious description of the data and used the criterion ΔAICc <2 (the difference between the AICc of a model and that of the model with the lowest AICc; Lebreton et al. 1992) to distinguish among candidate models. All models with and without covariates were analyzed using program MARK version 4.3 (White and Burnham 1999) using the logit and the multinomial logit link functions for the recovery probabilities and the state transition probabilities, respectively. Because existing goodness of fit tests for multistate models (i.e., Pradel et al. 2003) cannot be applied to data having absorbing states, we estimated the coefficient of overdispersion (or extra multinomial variation; Lebreton et al. 1992; see also White 2002) of the most complex among the set of predefined models by bootstrap. This coefficient of overdispersion was used to correct the values of AICc of all models derived from the most complex model and leading to the basic model (Quasi Akaike Information Criterion [QAIC]c). The division of the hunting season into 2 periods (September and October–January) in the basic model is in accordance with the changes in hunting pressure because September is the month with the strongest hunting pressure in our study site (when 68.2% of all recoveries occurred; François Bourguemestre, unpublished data).

Models with covariates
Once the basic model established, we formulated a set of covariate models combining individual standardized covariates and their interactions for both juvenile state transitions. The fitted models explored the extent to which each state transition probability could be explained by the individual or cohort-level covariates and/or their interactions by including them in the following linear logistic function:

$$\text{logit }\psi = \log\left(\frac{\psi}{1-\psi}\right) = \alpha + \beta_i \times \text{covar}_i + \beta_{i+1} \times \text{covar}_i + \ldots$$
$$+ \gamma_i \times \left(\text{covar}_i \times \text{covar}_{i+1}\right),$$

where ψ is a state transition probability, α is the intercept, β_i and γ_i are the slope for either an individual covariate i or an interaction between 2 covariates (denoted as $\text{covar}_i \times \text{covar}_{i+1}$), and i is the number of covariates in the model. We used the analysis of deviance to obtain an R^2-like measure of the best model including covariates (Skalski et al. 1993): and to estimate the percentage of deviance explained by each covariate. The sign, magnitude, and statistical significance of the each slope were used to test each individual covariate and their interactions on each state transition (i.e., $\psi_{A \to B}$ and $\psi_{A \to C}$).

Mixed effect models
Our models combine an individual covariate (body size index) and several covariates measured at the level of each re-

lease lake (lake area, cohort size, and hunting pressure) that could be a potential source of pseudoreplication. We have addressed this concern by fitting a linear mixed model with a binary response variable only for the juveniles reported dead during their first hunting season. Unlike the multistate recovery models, these logistic mixed models are based on recovered individuals and hence cannot model recovery probabilities. Individuals dead on site were coded as 0, whereas individuals dead outside were coded as 1. In these analyses, we used lake as a random factor to take into account for potential pseudoreplication (Pinheiro and Bates 2000), and time (a 2-level factor: i.e., September vs. October–January), hunting pressure, body size index, cohort size, and lake area as fixed explanatory variables. Starting with the full model containing all fixed parameters and 2-level interactions, we used backward model selection to select the most parsimonious model. All models were estimated using the library lmer in R 2.5.1.

RESULTS

Up to 35.2% of the 3733 individuals released between 2002 and 2004 were recovered in Brenne, 24.1% of those killed were recovered in a location other than the release lake (Tables 1 and 2), and only 0.2% of the banded birds were recovered outside Brenne region. Overall, 93.9% of recoveries corresponded to the releases on the same year. The high recovery rate over the study period together with the very low number of recoveries outside Brenne where wetland habitats are largely absent, suggest that this study provides a reasonably accurate picture of the spatial movements of mallards in our study site and at the regional level. However, the lower hunting pressure and the lower effort to report rings may also explain such low recovery rates outside Brenne. Median distance traveled by mallards from the release lake was 3.01 km (range = 0.1–91.4 km, $N = 316$). The distance traveled by the 6 ducks recovered outside of Brenne ranged from 34.0 to 91.4 km.

The basic model (Supplementary appendix 1) divided years into 3 periods (September, October–January, and the rest of the year), considered an age stratification between juvenile (year of release) and adults (subsequent years), and had recovery probabilities differing among years. Models containing other sex- and age-specific stratification of the recovery and state transition probabilities had lower empirical support than the basic model as indicated by the QAICc criterion (Supplementary appendix 1). The parameter estimates for the basic model are shown in Table 3. The probability of emigrating increased with time because it was greater in October–January than in September for the juveniles and also because the adult $\psi_{A \to C}$ was greater than the juvenile $\psi_{A \to C}$, whereas the reverse pattern occurred for the probability of remaining in the release site ($\psi_{A \to B}$) (Table 3). There was no significant variation in either $\psi_{A \to B}$ or $\psi_{A \to C}$ among years because the basic model did not include yearly changes in these

Table 3
Parameter estimates of the most parsimonious model without covariates shown in bold in the Supplementary appendix 1

Age	Time period	$\psi_{A \to B}$				$\psi_{A \to C}$			
		Estimate	SE	95% CI		Estimate	SE	95% CI	
Juveniles	September	0.183	0.018	0.150	0.222	0.080	0.013	0.058	0.109
	October–January	0.191	0.016	0.163	0.224	0.160	0.014	0.134	0.190
Adults	September	0.061	0.030	0.023	0.152	0.122	0.040	0.062	0.226
	October–January	0.094	0.025	0.055	0.156	0.188	0.034	0.130	0.265

The probabilities of remaining at ($\psi_{A \to B}$) and of emigrating ($\psi_{A \to C}$) from release site are shown for juveniles and adults for the months of September and October–January. CI, confidence interval.

rates (Supplementary appendix 1). The coefficient of over-dispersion $\hat{c}$ was found to be 1.43 and was used to correct the values of the AICc of all models.

The most parsimonious model having covariates (hereafter the covariate model) included body size, area of the release lake (as a proxy of resource availability), hunting pressure, cohort size (as a proxy of intraspecific competition), and the interaction between the last 2 covariates for juvenile transitions and no covariates for adult transitions (Supplementary appendix 2). We did not consider covariates for adult transitions because the overwhelming majority of recoveries corresponded to juveniles released the same year. Moreover, covariates such as cohort size are more likely to change over time because the number of ducks in each lake changes continuously due to mortality, emigration, and immigration.

Although the first 2 models of Supplementary appendix 2 are undistinguishable on the basis of ΔQAICc, we selected the additive model to test our predictions because it allows an easier interpretation of results. This covariate model explained 63.2% of the deviance of the basic model (i.e., without covariates) and, in decreasing order of importance, area of the release lake, body size, hunting pressure, cohort size, and the interaction between hunting pressure and cohort size explained, respectively, 21.4%, 21.4%, 21.3%, and 21.2% and 14.8% of deviance of the covariate model.

We also replaced hunting pressure with hunting frequency to assess the effect of disturbance. Hunting frequency was not correlated to the other 3 covariates. Models with hunting frequency were ranked similarly as the models with hunting pressure (data not shown). Thus, the correlations between hunting pressure and lake area or cohort size did not impact our model selection or our results. Our model selection (Supplementary appendix 2) was in agreement with the mixed logistic modeling approach based on dead individuals because the most parsimonious model was an additive model (hunt + body size + area + cohort) with interaction between time and cohort size, hunting pressure, and lake area (time × area + time × hunt + time × cohort, see Tables 4 and 5). The consistency of latter results with the structure of the covariate model would suggest that the potential of pseudoreplication in our analyses did not lead to spurious results.

Hunting pressure did not significantly differ between the release ($N = 32$) and recovery lakes ($N = 57$) (analysis of variance on log-transformed data: $F_{1,87} = 0.0001$, $P = 0.99$; average $= 27.4 \pm$ standard error [SE] $= 6.4$ vs. $23.0 \pm$ SE $= 3.0$, respectively). However, when comparing the hunting pressure of lakes of release and recovery for each individual, emigrating mallards came significantly more from release lakes having a high hunting pressure (Wilcoxon paired test: $W = 41804$, $P = 0.008$; $N = 232$).

In September, the $\psi_{A \to B}$ transition was significantly related to all covariates (Table 6). The probability of remaining and being killed at the release site ($\psi_{A \to B}$) was positively associated to hunting pressure in all months of the hunting season (Figure 2A,B, dark surfaces) and negatively to lake area. Individuals released with a few number of conspecifics (small cohort size: Figure 2C) in a small lake and faced to high hunting pressure were more likely to be killed on site (Figure 2). Emigration rate ($\psi_{A \to C}$) in September was higher for large lakes and low hunting pressure (Figure 2A), whereas during the remaining months of the hunting season (October–January) this transition was positively (but nonsignificantly, see Table 6) related to hunting pressure (Figure 2B, white surface). Whatever the time period considered, emigration rate was negatively but nonsignificantly related with cohort size (Figure 2C,D). Large-bodied individuals were significantly more likely to stay, whereas conversely, small-bodied individuals were (nearly significantly) more likely to emigrate from the release lake (Figure 3); the latter result was consistent across the entire hunting season and for all years (Table 6).

DISCUSSION

This study investigated the large-scale temporal patterns of emigration in released juvenile mallards. The specific conditions of our study site (i.e., tightly managed for hunting, "predators" having restricted access only to single lakes during the entire season, high recovery rates, and quantification of explanatory covariates) defined a quasi-experimental system that allowed examine the proximate ecological factors involved in emigration under natural conditions and over large spatial scales. To depict whether emigration decisions were due to predation risk or local competition, we draw out 2 main hypothesis and predictions. The finding that emigration rate was strongly and positively related to lake size and negatively (but not significantly) related to cohort size in September would lead to reject the role of intraspecific competition in determining mallard emigration. However, larger individuals tended to emigrate less than smaller ones. The fact that the effect of hunting pressure changed between 2 time periods (negative slope in September and positive afterward) would suggest that birds reacted to hunting pressure after the opening of the hunting season. In addition, we found

Table 4

Parameter values of the additive model showed in the Supplementary appendix 2

Time period	Parameter	$\psi_{A \to B}$				$\psi_{A \to C}$			
		Estimate	SE	95% CI		Estimate	SE	95% CI	
September	Intercept	−1.113	0.312	−1.724	−0.502	−2.434	0.448	−3.312	−1.556
	Body size	0.004	0.001	0.002	0.007	−0.002	0.002	−0.005	0.002
	Hunting	0.028	0.007	0.015	0.041	−0.006	0.010	−0.026	0.014
	Cohort	−0.008	0.003	−0.013	−0.002	−0.002	0.004	−0.009	0.005
	Lake area	−0.072	0.018	−0.106	−0.038	0.050	0.025	0.001	0.099
October–January	Intercept	−0.684	0.216	−1.107	−0.260	−1.479	0.244	−1.957	−1.002
	Body size	0.003	0.001	0.001	0.005	−0.001	0.001	−0.003	0.001
	Hunting	0.001	0.005	−0.009	0.011	0.001	0.005	−0.009	0.012
	Cohort	−0.002	0.001	−0.004	0.001	0.001	0.001	−0.001	0.003
	Lake area	−0.042	0.015	−0.072	−0.012	−0.007	0.014	−0.035	0.022

The effect of the covariates on the probabilities of remaining at ($\psi_{A \to B}$) and of emigrating ($\psi_{A \to C}$) from release site are shown for juveniles for the months of September and October–January. These parameter estimates were used to generate the predicted curves shown in Figures 2 and 3. All covariates were standardized prior to the analyses and parameters estimates are given after back transformation (Cooch and White 2008). CI, confidence interval.

Table 5

Results of model selection from mixed logistic models on emigration probability using only the recovered individuals (individuals dead on site were coded as 0, whereas individuals dead outside were coded as 1)

Models	Degrees of freedom	AIC	ΔAIC
Hunt + size + cohort + area + time + hunt × time + cohort × time + area × time	10	762.52	0.00
Hunt + size + cohort + area + time + hunt × time + cohort × time + area × time + size × time	11	763.13	0.61
Hunt + cohort + area + time + hunt × time + cohort × time + area × time	9	764.17	1.65
Hunt + size + cohort + area + time + hunt × time + cohort × time	9	787.89	25.37
Hunt + size + cohort + area + time + hunt × time + area × time	9	788.30	25.78
Hunt + size + cohort + area + time + hunt × time	8	797.03	34.51
Hunt + size + cohort + area + time + hunt × time + size × time	9	798.40	35.88
Hunt + size + cohort + area + time	7	799.34	36.82
Size + cohort + time	5	802.10	39.58
Cohort + time	3	807.66	45.14
Time	3	829.59	67.07
Hunt + time	4	830.80	68.28
Full model	33	855.51	92.99
Null model	2	911.00	148.48

Lake identity was included as a random factor to take into account for potential pseudoreplication (Pinheiro and Bates 2000). Time (September vs. October–January), hunting pressure (hunt), body size index (size), cohort size (cohort), and lake area (area) were used as fixed explanatory variables. The index of overdispersion (c-hat) was 0.96 for the null model and 1.61 for the most parsimonious one.

that emigrating birds were more likely to come from lakes having a higher hunting pressure. All these findings suggest that emigration result from the interplay between the effects of predation risk and competition avoidance.

Effect of predation risk on emigration decisions

For the sake of simplicity and to assess the importance of each covariate independently, we mostly focused on the results from the additive model (the 2 first models received almost identical (ΔQAICc < 2) empirical support from the data; Supplementary appendix 2). Nevertheless, a significant interaction between hunting pressure and cohort size remains in 1 of the 2 more parsimonious models. This interaction was mainly due to a bimodal distribution of the values for the interaction between these cohort-level covariates that were either strongly negative or positive with no intermediate values around the average. The 2 modes corresponded to lakes having different strategies of management of resource stocking and hunting pressure that determined contrasting behavioral responses of the locally released mallards. On the one hand, the positive values of the interaction corresponded to individuals belonging to 2 lakes in 2 consecutive years that had large release events (average 293.2 individuals per lake ± SE = 61.2), high hunting pressure (average 104 hunters per lake per month ± SE = 16), and a large size (23.1 ha ± SE = 9.3). They accounted for 25% of all releases and 39.9% of all recoveries in Brenne between 2002 and 2004. On the other, the negative values of

Table 6

Parameters estimates of the most parsimonious model (shown in bold in Table 5)

Covariate	Estimate	SE	z value	P value
Intercept	−3.983	0.996	−3.998	<0.001
Hunt	−0.085	0.021	−4.156	<0.001
Size	−0.002	0.001	−1.941	0.052
Cohort	0.035	0.006	6.074	<0.001
Area	0.182	0.058	3.146	0.002
Time	3.899	0.656	5.940	<0.001
Hunt × time	0.082	0.013	6.208	<0.001
Cohort × time	−0.030	0.006	−4.979	<0.001
Area × time	−0.132	0.025	6.208	<0.001

the interaction between hunting pressure and cohort size corresponded to individuals from the remaining 30 small lakes (9.9 ha ± SE = 1.7) that had small release cohorts (average 59.7 individuals per lake ± SE = 6.8), moderate hunting pressure (average 23 hunters per lake per month ± SE = 5). Nevertheless, individuals were more likely to emigrate when the release cohorts were small and lake area was large, thus illustrating the dilution effect of hunting (risk spreading) for larger cohorts (e.g., Hamilton 1971). Besides its direct mortality effect, hunting is also a source of disturbance for many waterfowl species (review in Madsen and Fox 1995) and it is known to promote escaping behavior (Béchet et al. 2004). Hunting frequency (our proxy for disturbance) and hunting pressure had the same effect on emigration transitions. The hunting (frequency or pressure) covariate was mostly related to the probability of being killed on site. One could have expected the effect of disturbance on emigration rate to be greater in small lakes at any hunting pressure, but we found lake area to be positively and significantly related to emigration rate. The latter suggests that for the actual hunting pressure in our study site, the detection rate of mallards by hunters was relatively high in small lakes so that the strong direct mortality effect of hunting probably concealed its impact as disturbance. Although our results suggest that bird emigration is related to hunting effects rather than competition, we were unable to separate these 2 potential drivers of emigration. Additional information on hunting disturbance (e.g., the number of shots fired) would have helped to disentangle the direct and indirect effects of predation risk on emigration.

Effect of body size on emigration decisions

Our index of phenotypic variation reflected more adult body size than body condition at the juvenile stage. Structural body size in birds is largely determined by developmental stress (i.e., the amount and quality of food eaten) during the growing period (Larsson et al. 1998; Naguib et al. 2004). The age-corrected body weight measured during the growing phase may thus reflect the quantity and quality of resources received by mallards during early juvenile stages that is known to affect body size of full-grown individuals (Larsson et al. 1998). Several studies have shown that activity levels increases in undernourished birds (e.g., Astheimer et al. 1992), a physiological state that stimulates glucocorticoid secretion (Cherel et al.
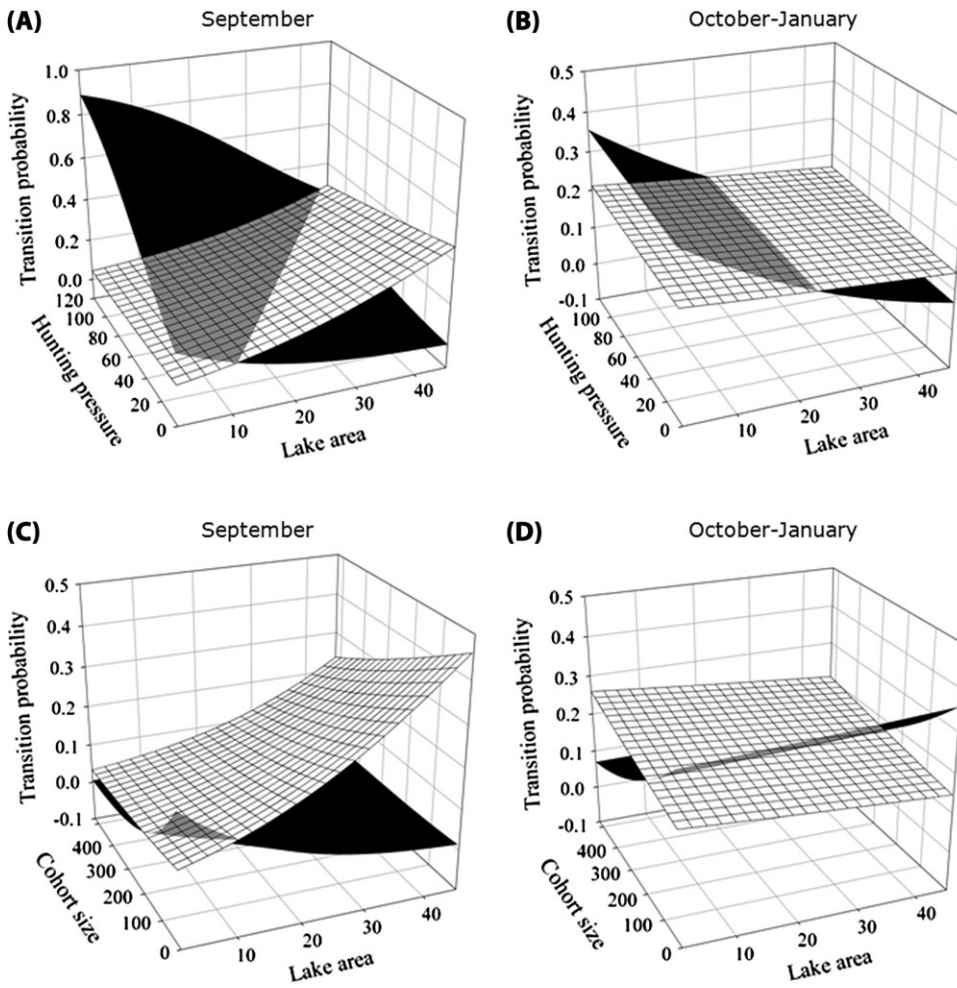
Figure 2
Predicted values of the monthly probabilities of remaining at the release site (black) and of emigration (white) of released mallards in Brenne between 2002 and 2004 as a function of lake area, cohort size, and hunting pressure. The surfaces were generated using the additive model (showed in bold in Supplementary appendix 2 and with parameter values as given in Table 3) for the average values of body size, hunting pressure, or cohort size when these covariates are not presented. Plots on the left panel are those for September (A, C) and those on the right panel correspond to October–January (B, D). All covariates were standardized prior analyses and back transformed to draw out the graphs. The confidence intervals are not shown for clarity, but they are available in Table 6.

1988), and increases the tendency to leave the natal habitat (e.g., Belthoff and Dufty 1998). Our results show that emigration is more important for smaller individuals. We previously stated that our 2 hypotheses were nonmutually exclusive and that emigration would result from both predation risk and competition avoidance. Both competition for food and dominance hierarchies could be involved in explaining why smaller individuals would emigrate more than larger ones. Brenne

is an intensively managed area that is largely predation-free habitat between the releases in July and the opening of the hunting season in September. Thus, juvenile mallards roosting in these predation-free habitats were probably surprised by the sudden start of hunting, and smaller individuals would be more likely to escape from predation risk (or would have already emigrated), whereas larger individuals suffered high mortality at the release lakes. The fact that emigration rate was
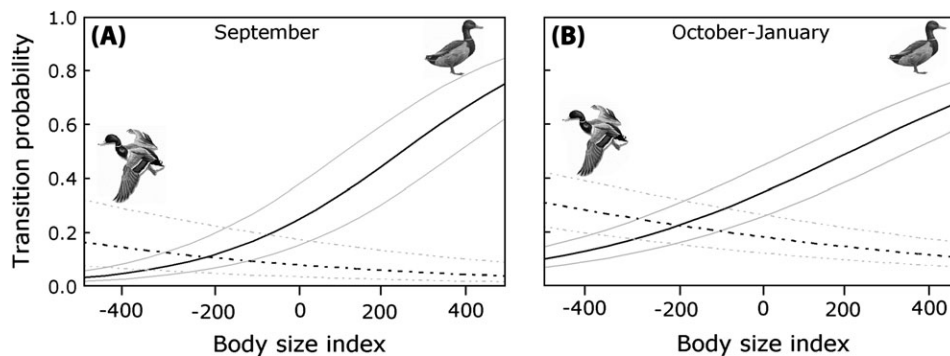
Figure 3
Predicted values of the monthly probabilities of remaining at the release site (solid lines: standing duck) and of emigration (dotted lines: flying duck) of juvenile released mallards according to body size index (standardized corrected weight) and months (September in [A] vs. October–January in [B]). The curves were calculated using the additive model (showed in bold in Supplementary appendix 2 and whose parameter values are those shown in Table 3) for the average values of lake, hunting pressure, and cohort size. The confidence intervals are shown in gray. All covariates were standardized prior analyses and back transformed to draw out the graphs.

higher for birds coming from larger lakes tend to reinforce this explanation because larger lakes offered greater movement opportunities that may ultimately help to escape from hunting risk (a prerequisite to emigrate).

Although hunting pressure and consequently local mallard abundance varied during the hunting season, the effect of phenotypic variation on emigration decisions were likely to be preserved during the hunting season. The latter may explain the more pervasive and consistent effect of body size during the hunting season compared with the shifts in the observed effects of hunting pressure and cohort size on transition probabilities.

Previous studies with waterfowl have shown that individuals culled around protected areas were in lower body condition than individuals remaining in protected areas (Dufour et al. 1993; Heitmeyer et al. 1993; Guillemain et al. 2007). Our results agree with these previous studies if one considers all lakes (including the released areas) in our study site as protected habitats before the start of the hunting season. Although local movements are generally thought to be motivated by feeding requirements, in our case, emigration is also the result of hunting activity. However, in any of these situations, individuals that are most likely to redistribute themselves over space are generally those having a low body condition (see for instance, finding of Ekman et al. (2002) that dispersal rates of the Siberian Jays (*Perisoreus infaustus* L.) were higher for smaller and subordinate individuals. In birds, regardless of the mechanism involved in promoting emigration, phenotypic traits such as body condition or body size may appear to modulate dispersal (and thus emigration) behavior. In birds, the rate of dispersal could either decline (e.g., Belthoff and Dufty 1998; Ekman et al. 2002; this study), increase (van der Jeugd 2001) or even have a quadratic relation with individual quality (Barbraud et al. 2003; Blums et al. 2003). Given that individual phenotype seems to shape the emigrating response, understanding the mechanistic links between body size or condition, behavioral dominance, and food availability remains a challenge for further experimental studies.

SUPPLEMENTARY MATERIAL

Supplementary material can be found at http://www.beheco.oxfordjournals.org/

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