

Contrasting patterns of survival and dispersal in multiple habitats reveal an ecological trap in a food-caching bird

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Abstract A comprehensive understanding of how natural and anthropogenic variation in habitat influences populations requires long-term information on how such variation affects survival and dispersal throughout the annual cycle. Gray jays *Perisoreus canadensis* are widespread boreal resident passerines that use cached food to survive over the winter and to begin breeding during the late winter. Using multistate capture-recapture analysis, we examined apparent survival and dispersal in relation to habitat quality in a gray jay population over 34 years (1977–2010). Prior evidence suggests that natural variation in habitat quality is driven by the proportion of conifers on territories because of their superior ability to preserve cached food. Although neither adults (>1 year) nor juveniles (<1 year) had higher survival rates on high-conifer territories, both age classes were less likely to leave high-conifer territories and, when they did move, were more likely to disperse to high-conifer territories. In contrast, survival rates were lower on territories that were adjacent to a major highway compared to territories that did not border the highway but there was no evidence for directional dispersal towards or away from highway territories. Our results support the notion that natural variation in habitat quality is driven by the

proportion of coniferous trees on territories and provide the first evidence that high-mortality highway habitats can act as an equal-preference ecological trap for birds. Reproductive success, as shown in a previous study, but not survival, is sensitive to natural variation in habitat quality, suggesting that gray jays, despite living in harsh winter conditions, likely favor the allocation of limited resources towards self-maintenance over reproduction.

Keywords Gray jays · Highways · Multistate capture–recapture · *Perisoreus canadensis* · Seasonality

Introduction

Understanding how natural and human-altered habitats influence fitness and population dynamics requires detailed knowledge of how habitat variability affects survival and dispersal throughout the annual cycle (Fretwell 1972; Silllett et al. 2000; Clobert et al. 2001; Bowler and Benton 2005; Welch et al. 2008). Unfortunately, for the vast majority of species we have little information on how these demographic parameters might vary between seasons and habitats because most studies are less than 5 years in duration, take place over short time periods in relatively uniform habitat, and are often based on unmarked animals. Nowhere is this more apparent than in northern ecosystems, where most areas are difficult to access and data are typically only collected during a short growing season (but see Krebs et al. 2000). There is a pressing need to understand both the basic ecology of northern species and how they will respond to environmental change because high-latitude ecosystems, such as the boreal forest, are under increasing threat from climate change, habitat loss and habitat degradation (McGuire et al. 2007; Soja et al. 2007).

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In this paper, we estimated seasonal survival and dispersal between territories in a population of gray jays *Perisoreus canadensis*, a resident corvid that occupies boreal forest throughout North America (Strickland and Ouellet 2011). Gray jays are relatively long-lived birds that form multi-year pair bonds, reside in stable, year-round territories, and rely on cached food for both overwinter survival and breeding (Strickland 1969; Strickland and Ouellet 2011). The timing of breeding is one of the most striking characteristics of this species because breeding pairs typically begin building nests in late February/early March and fledge young in late April/early May (Strickland and Ouellet 2011). In June, all but one of the juveniles (usually two of three) disperse from their natal territory while the dominant juvenile may delay dispersal until the next summer or even later (Strickland 1991). Both “classes” of juveniles fill breeding vacancies when available. When disappeared breeders are not promptly replaced, the widowed adults may also disperse, either to fill a same-sex vacancy or to evict an established breeder elsewhere (D. S., D. R. N., unpublished data).

Between 1977 and 2010, we monitored a marked population of gray jays at the southern edge of their range in Algonquin Park, Ontario, Canada. Previous work has shown that the proportion of occupied territories in this population has declined by >50 % over the last 33 years (Waite and Strickland 2006; Strickland et al. 2011). Using multistate mark-recapture models, we estimated apparent survival and transition probabilities (dispersal rates between territories) over two time periods of the year [spring/summer (March to mid-October) and fall/winter (mid-October to February)] in both juveniles (<1 year) and adults (>1 year) to examine multiple hypotheses to explain variation in habitat quality and seasonality.

First, prior evidence suggests that habitat quality in this population is, at least partly, related to the proportion of coniferous trees on territories because of their superior ability to preserve cached food over deciduous trees (Strickland et al. 2011). Simulated caches placed on the bark of conifers lose less weight over 1–4 months compared to caches on deciduous trees and gray jays have higher reproductive success on territories with a high proportion of conifers (Strickland et al. 2011). Following this, we predicted that individuals occupying high-conifer territories would have the highest survival rates and would be the least likely to leave their territories. Among jays that did disperse, we predicted that individuals would show directional movement towards high-conifer habitats.

Second, we examined the hypothesis that the presence of roads influences gray jay abundance by causing mortality from vehicle collisions. Road collisions have been estimated to represent a significant source of avian

mortality (Forman and Alexander 1998; Coffin 2007), including in a closely related species (Mumme et al. 2000), and carcasses of marked gray jays recovered from beside a highway that runs through our study area (D. S., unpublished data) suggest that roads may significantly impact population-level survival rates. Thus, we predicted that survival would be lower on territories that were adjacent to the highway compared to territories that did not border the highway. If jays are able to recognize roads as a potential threat, then we predicted individuals would be more likely to disperse away from highway territories and towards non-highway territories. Alternatively, roads may act as a type of equal-preference ecological trap (Robertson and Hutto 2006), whereby animals have lower fitness in altered habitats but show a neutral preference between the altered and natural habitat. In the case of gray jays, this hypothesis would predict that, despite suffering high mortality rates near highways, individuals would be neither repelled nor attracted by highway habitats. This equal-preference ecological trap can be contrasted with the supernormal ecological trap (Robertson and Hutto 2006), which assumes that animals both have lower fitness in altered habitats and are attracted to these habitats.

We also examined two competing hypotheses to explain seasonal variation in survival. The first was that gray jays have higher survival rates during the fall/winter because of higher mortality rates during the spring and summer from migratory raptors that breed in Algonquin Park. In addition, our prior estimates based on the number of individuals observed across seasons (i.e., that do not take into account recapture probability) suggest that jays have higher survival during the fall/winter (Strickland 1992; Strickland and Ouellet 2011). Alternatively, gray jays may have lower survival rates during the fall/winter because they rely on perishable cached food that is presumably less abundant than fresh food during the spring/summer. Gray jays consume a wide variety of food items, including arthropods, berries, fungi, eggs and vertebrate flesh from a number of sources (Strickland 1969), so they are likely not food-limited during the growing season.

Materials and methods

Study species and data

From 1977 to 2010, we studied a marked population of resident gray jays in the southwestern portion of Algonquin Park, Ontario (45°35'N, 78°30'W). The study area is located on the southern edge of the gray jay range within the transition zone between Great-Lakes-St. Lawrence deciduous hardwood forest and northern boreal forest.

Each year, we conducted two population censuses: the spring census between 15 February and 15 March, at the beginning or shortly before the start of nest building and the fall census that occurred on or near 15 October, when all birds are well past molt and are actively caching food for the winter (Strickland and Ouellet 2011). For each census, territories (~ 160 ha) were visited multiple times to record the occupants and capture any individuals that had not been previously marked. All individuals were caught using a walk-in potter trap and banded with a unique combination of a U.S. Fish and Wildlife Service aluminum leg band and two or three plastic color leg bands. During the breeding season, nests were found on all territories (success rate of finding nests: 95–100 %) and nestlings were banded on day 11. Visitation to nests after this period can cause premature fledging, which typically occurs on day 23. Thus, the “juvenile” survival estimate encompasses the second half of the nestling period. However, from our observations later on in the breeding season, there are very low predation rates in the latter stages of nesting. Jays were considered “juveniles” until the end of their first year (spring census period), after which they were incorporated into the “adult” age category (>1 year; but see calculation of transition probabilities below).

Following Strickland et al. (2011), territories were classified into one of three habitat quality classes based on the percent of conifer trees: low, 0–40 %; medium, 40–58 %; high, 58–100 %. Each territory was also classified as being adjacent or not adjacent to a major highway (Highway 60) that runs through the study area. To adjust for variation in observation effort of gray jays during our study, we calculated observer survey effort as the number of territories surveyed during each census period divided by the maximum number of territories surveyed. Observer effort was used as a linear covariate to explain recapture (re-sighting) probability.

Model building

Multistate models produce probability estimates for three parameters: apparent survival (Φ), recapture (p), and transition (Ψ). Using multistate models with six habitat classes (three conifer classes and two highway classes), two age classes (adult, juvenile), two seasons (spring/summer, fall/winter), and 34 years resulted in a saturated model that was too computationally demanding. We therefore conducted the analysis in two stages. The first stage included age, season, year, and conifer class. The second stage carried over the best-supported model, removed the effect of conifer class on Ψ , and then added the effect of highways for Φ , p , and Ψ . To avoid an excessive number of models and aid in simplifying inferences, we considered model selection in a forward step-wise approach where we

included variation in only one parameter (Φ , p , Ψ) in a single stage while the other parameters remained consistent from the previous step (Redmond and Murphy 2011). We included single explanatory variables first and then considered additive and interactive models with those variables that held the most support when considered in isolation. Model notation follows that of Lebreton et al. (1992).

“Transition” refers to movement among the different habitat classes considered in each analysis given that an individual has survived the preceding time interval (Hestbeck et al. 1991). In our case, these habitat classes were either the conifer class (conifer) or whether territories were adjacent to the highway (hwy) or not adjacent to the highway (nonhwy). Transition was assumed to occur at the end of the time interval where there were differences in survivorship between habitat classes, but this assumption can be relaxed if survival is shown not to vary between habitat classes (Brownie et al. 1993, Hestbeck 1995). Although transition probability among all observable discrete states sums to 1, parameter and variance estimates of transition are only available for movement between states and not for remaining in the previously occupied habitat class. Therefore, the probability of remaining in the previously occupied site was calculated by subtraction from unity (Lebreton and Pradel 2002).

We began with constant survival (Φ) and recapture probability (p) to determine the most parsimonious parameterization of transition probability. We considered age (Ψ_{age}), season (Ψ_{season}), and either conifer (Ψ_{conifer}) or highway (Ψ_{hwy}), as well as two-way and three-way comparisons. When conifer or highway class were included in models describing transition, it is important to note that there are several possible ways to constrain the movement estimates between the classes individuals depart from and those which they move to. We only considered parameterizations where the estimates varied independently between the departure and receiving territory. However, transition estimates could be constant between departure sites to a single receiving site or constant from a single departure site to different receiving sites. To reduce model complexity, we did not consider temporal variation in transition because jays do not move frequently enough between time steps, which would result in low power to detect temporal effects.

For transition probabilities of juveniles, we were interested in dispersal from an individual’s natal habitat to their first breeding habitat. However, juvenile jays have a unique dispersal pattern (Strickland 1991). Sub-dominant offspring (usually two of the three young born in a given year) disperse in their first summer and are rarely observed to recruit into the population, whereas dominant offspring are usually seen with their parents during our fall census and

almost always delay dispersal until the following summer after young born in the following year become independent (Strickland 1991; Strickland and Ouellet 2011). Thus, we constrained (dominant) juveniles from recruiting, and therefore transitioning from natal to breeding territories, until they were at the end of their 1st year (2nd potential breeding season). The result was that, at any time step, only about one-third of the juveniles in the population are in transition (the other two-thirds were young at 6 and 12 months of age that were constrained to remain on their natal territory) to a breeding territory. For this reason, our transition probability estimates to breeding territories did not sum to 1 for this age group. Instead, the difference was the probability of juveniles being “constrained” from departing the natal territory.

Seasonal estimates of apparent survival corresponded to spring/summer (March to mid-October) and fall/winter (mid-October to Feb) and occurred between the spring and fall censuses. Apparent survival and recapture probabilities were, therefore, modeled during these intervals. In juveniles, age and season were confounded because jays raise a single brood and juveniles captured in the fall must be 6 months old. As a result, parameter estimates for 6-month-old and 12-month-old juveniles in an age-only model were equivalent to parameter estimates for juveniles in a season-only model. For this reason, survival models that included Φ_{age} as the only explanatory variable had equal parameter estimates for jays in their first spring/summer and fall/winter, additive models of age and season ($\Phi_{\text{age+season}}$) estimated different intercepts for adults and juveniles and had equal slopes to describe seasonal effects,

while interaction models ($\Phi_{\text{age} \times \text{season}}$) provided independent intercept and slope estimates for both adult and juveniles in each season.

We used program MARK (White and Burnham 1999) to parameterize models and then used the Akaike information criterion likelihood value adjusted for small sample sizes (AICc) to rank competing models (Burnham and Anderson 2002). Models within $<3 \Delta\text{AICc}$ units from the top model can be considered as competing models to describe variation in survival given the data (Burnham and Anderson 2002). We used likelihood ratio tests to determine the significance of specific factors in competing nested models. Akaike weights provided the cumulative support of a model given all competing models while the model likelihood measured the relative support of a given model with respect to the top model in a the candidate list. We derived real parameter estimates from MARK to plot survival, recapture and movement relationships with respect to our explanatory variables for the best-supported model. All parameter estimates are shown using the mean and 95 % confidence interval.

Results

Effects of season, conifer class, and age

Under constant terms for survival and recapture probability, transition was best explained by variation by conifer class (Table 1). Overall, this model held more than twice the level of support than a more complex

Table 1 Results of model selection for transition (Ψ), recapture (p) and survival probabilities (Φ) with respect to effort (linear relationship to proportion of total territories surveyed), age (juvenile, adult), season (spring/summer, fall/winter), and conifer (% conifer on territories, three classes; see “Materials and methods”), and time (year) for gray jays from Algonquin Park, Ontario, 1977–2010. “(.)”

represents a constant or intercept-only model. The change in Akaike information criterion likelihood value adjusted for small sample sizes (AICc), the Akaike weight (w_i), model likelihood (l_i), number of model parameters (K), and model deviance (*Deviance*) are presented for each model

Term	Model	ΔAICc	w_i	l_i	K	Deviance
Ψ^a	$\Phi(.) p(.) \Psi(\text{age} + \text{conifer})$	0	0.668	1	13	38,031.3
	$\Phi(.) p(.) \Psi(\text{age} + \text{season} + \text{conifer})$	1.81	0.270	0.405	14	38,031.0
	$\Phi(.) p(.) \Psi(\text{age} \times \text{conifer})$	4.74	0.063	0.093	19	38,023.9
p^b	$\Phi(.) p(\text{effort}) \Psi(\text{age} + \text{conifer})$	0	0.286	1	14	38,028.5
	$\Phi(.) p(\text{season} \times \text{effort}) \Psi(\text{age} + \text{conifer})$	0.19	0.260	0.909	16	38,024.6
	$\Phi(.) p(.) \Psi(\text{age} + \text{conifer})$	0.78	0.194	0.678	13	38,031.2
	$\Phi(.) p(\text{season} + \text{effort}) \Psi(\text{age} + \text{conifer})$	1.35	0.145	0.508	15	38,027.8
	$\Phi(.) p(\text{season}) \Psi(\text{age} + \text{conifer})$	1.83	0.115	0.402	14	38,030.3
	$\Phi(\text{age} \times \text{season}) p(\text{effort}) \Psi(\text{age} + \text{conifer})$	0	0.972	1	17	36,644.6
Φ^c	$\Phi(\text{age} + \text{season}) p(\text{effort}) \Psi(\text{age} + \text{conifer})$	11.77	0.003	0.003	16	36,658.4

^a AICc value of the top model in this step was 39,944.06

^b AICc value of the top model in this step was 39,943.28

^c AICc value of the top model in this step was 38,565.50

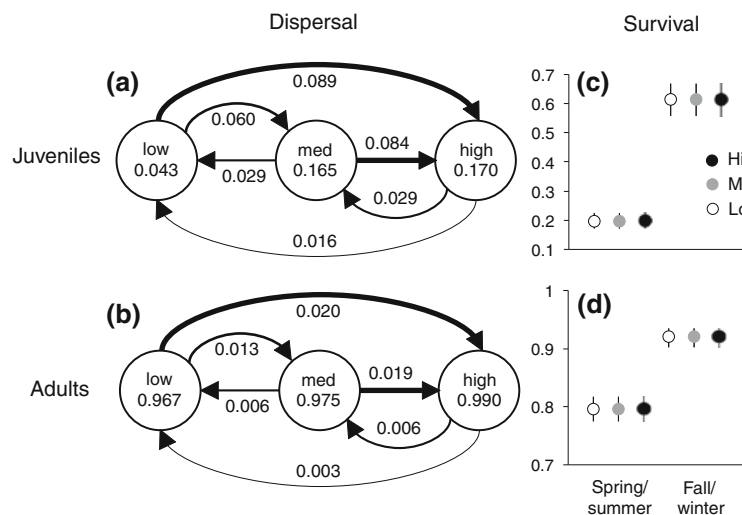


Fig. 1 Dispersal or transition probabilities (**a, b**) in relation to the percent conifer on territories [0–40 % (*low*), *medium* 40–58 % (*medium*), 58–100 % (*high*)] and apparent survival (**c, d**) in relation to conifer class (as above) and season of both juvenile (**a, c**) and adult (**b, d**) gray jays in Algonquin Park, ON. Transitions in juveniles refer to dispersal from natal habitat to first breeding habitat, which occurred in year 2. Transition probabilities presented for immature jays are less than 1 because young jays were constrained to remain on their natal or adoptive territory until they reached the age of transition

(see “Materials and methods” for details). All estimates are based on the top model from Table 1. **a, b** Thickness of the arrows corresponds to the magnitude of the estimate (for juveniles, thinnest arrows 0.010–0.015, thickest arrows 0.05–0.10; for adults, thinnest arrows 0–0.005, thickest arrows 0.015–0.020) and numbers inside circles represent probability of transitioning to the same habitat type. **c, d** Error bars are \pm 95 % confidence intervals. SE for estimates for transition probabilities are in Table S1

additive model that included season and conifer class (Table 1). Both models also included the covariate age. Juveniles that recruited into the study area were most likely to recruit into a conifer class similar to their natal habitat type. The exception was for juveniles born in low-conifer habitat, who were more likely to disperse to territories with higher proportions of conifers than to disperse to territories that were the same as their natal habitat (Fig. 1a; Supplementary Material, Table S1). Among the juveniles that dispersed from high- and medium-conifer habitats, individuals tended to disperse to territories with the next highest proportion of conifers (Fig. 1a; Supplementary Material, Table S1). Dispersal patterns in adults were similar (Fig. 1b; Supplementary Material, Table S2). Individuals dispersing from high-conifer territories were more likely to remain in the same habitat type compared to individuals dispersing from territories with a lower proportion of conifers (Fig. 1b; Supplementary Material, Table S2). When adults did disperse to a different habitat, they moved at higher rates and directionally to territories with higher proportions of conifers: adults from high-conifer habitats were almost twice as likely to move to medium- compared to low-conifer habitat; adults from medium-conifer habitat were three times more likely to move to high-conifer compared to low-conifer habitat; and adults from low-conifer habitat were most likely to move to high-conifer habitat (Fig. 1b, Supplementary Material, Table S2).

Carrying the best parameterization of transition forward, we then held survival constant and tested variation in recapture probability. The model that included a linear term of observer effort (not shown, but see Supplementary Material, Fig. S1b for estimates derived from the highway model) held more support than one based on seasonal variation but only slightly more support than the model with constant recapture probability ($\chi^2 = 2.79$, $df = 1$, $P = 0.0949$; Table 1). Although the additive and interactive models of season and effort held some support with lower recapture probability in spring than fall, the high degree of model uncertainty for recapture probability suggested that this parameter was consistent over time (Supplementary Material, Fig. S1a).

With recapture probability and transition probability constrained as above, there was strong support for a model with variation in survival by age over a constancy model (Table 1; Fig. 1c, d). There was no variation in survival between habitat classes (Fig. 1c, d) and this model (Φ_{habitat}) did not significantly explain more variation in the data from a constancy model ($\chi^2 = 3.361$, $df = 2$, $P = 0.19$; Table 1). When temporal variation was constrained to two seasons it held substantially more support than the time-only model (Table 1). An interactive model between season and age held more support than a simpler additive model (Table 1), and this was primarily due to the large difference in apparent survival in juveniles between seasons (Fig. 1c, d).

Table 2 Results of model selection for Ψ , p and Φ with respect to highways (*hwy*). We retained the top model from Table 1 [$\Phi(\text{age} \times \text{season}) p(\text{effort}) \Psi(\text{age} + \text{conifer})$] but eliminated conifer as an explanatory variable for Ψ and then assessed the effect of *hwy* on the parameters of interest. The change in AICc units, w_i , l_i , K and

Term	Model	ΔAICc	w_i	l_i	K	Deviance
Ψ^a	$\Phi(\text{age} \times \text{season}) p(\text{effort}) \Psi(\text{age} \times \text{hwy})$	0	1	1	12	19,497.9
p^b	$\Phi(\text{age} \times \text{season}) p(\text{hwy} + \text{effort}) \Psi(\text{age} \times \text{hwy})$	0	0.791	1	13	19,493.3
	$\Phi(\text{age} \times \text{season}) p(\text{effort}) \Psi(\text{age} \times \text{hwy})$	2.66	0.209	0.264	12	19,497.9
Φ^c	$\Phi(\text{age} \times \text{season} + \text{hwy}) p(\text{hwy} + \text{effort}) \Psi(\text{age} + \text{hwy})$	0	0.776	1	14	19,488.9
	$\Phi(\text{age} \times \text{season}) p(\text{hwy} + \text{effort}) \Psi(\text{age} + \text{hwy})$	2.37	0.234	0.305	13	19,493.3
	$\Phi(\text{age} \times \text{season} \times \text{hwy}) p(\text{hwy} + \text{effort}) \Psi(\text{age} + \text{hwy})$	13.17	0.001	0.001	21	19,487.9

^a AICc value of the top model in this step was 21,732.61

^b AICc value of the top model in this step was 21,729.95

^c AICc value of the top model in this step was 21,727.58

Effects of highways

To test the influence of highway on survival, recapture, and dispersal, we carried the top model from the above analysis but removed the effects of conifer habitat on transition probability to form the model ($\Phi_{\text{age} \times \text{season}} p_{\text{effort}} \Psi_{\text{age}}$). Adding the effect of highway in transition probability yielded an improvement in model fit (Table 2). Both juveniles (when they recruited) and breeding adults were more likely to remain on the habitat they were on previously (Fig. 2a, b; Supplementary Material, Tables S3, S4). However, when either age class did move, there was no evidence of directional dispersal away or toward highway territories (Fig. 2a, b; Supplementary Material, Tables S3, S4).

There was an improvement in the model fit when recapture probability was explained by the effect of highway (Table 2). Recapture rates were 2.5 % higher for individuals on territories adjacent to the highway compared to those away from the highway (Supplementary Material, Fig. S1b).

The top model explaining variation in survival included an additive effect of highway and was about three times more likely than if highway was ignored (Table 2). The pattern of survival between juvenile and adult jays in spring/summer and fall/winter was similar to the base model described above (Table 1; Fig. 1c, d). However, survival was consistently lower for jays on territories adjacent to highways (Fig. 2c, d). Survival during the spring/summer was 4 % lower on highway territories compared to non-highway territories for both juveniles and adults. In the fall/winter, mortality increased by 6 % for juveniles adjacent to highways and 2 % for adults.

deviance are presented for each model. Interactive models (shown with \times) indicate independent estimates for each grouping of the factor, while additive models (+) are dependent estimates that share a common slope but have different intercepts. For abbreviations, see Table 1

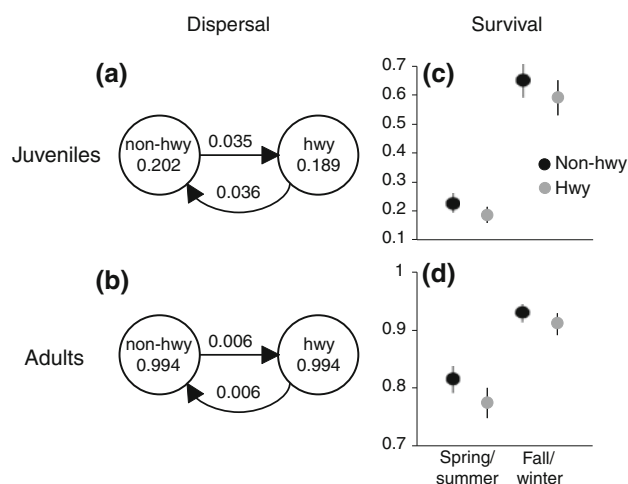


Fig. 2 Dispersal or transition probabilities (**a**, **b**) in relation to the presence of a highway [*hwy* (territories that border the highway); *non-hwy* (territories that do not border the highway)] and apparent survival (**c**, **d**) in relation to *hwy* (as above) and season of both juvenile (**a**, **c**) and adult (**b**, **d**) gray jays in Algonquin Park, ON. Transition probabilities for juveniles are the same as in Fig. 1. All estimates are based on the top model from Table 2. **a**, **b** Thickness of the arrows corresponds to the magnitude of the estimate (see Fig. 1) and numbers inside circles represent probability of transitioning to the same habitat type. **c**, **d** Error bars are \pm 95 % confidence intervals. SE for estimates for transition probabilities are in Table S2

Discussion

Our results over a 34-year time period demonstrate clear and contrasting effects of anthropogenic and natural variation in habitat quality on the survival and dispersal of a boreal resident animal. Although we found no evidence for a relationship between survival and the proportion of conifers on territories, adults and juveniles in high-conifer habitats were less likely to disperse away from high-conifer

territories and, among those that did disperse, individuals showed consistent directional movement towards high-conifer habitats. Perhaps the strongest evidence for variation in habitat quality came from the transition probabilities in medium-conifer habitats, where both adults and juveniles were three times more likely to move towards high-conifer territories compared to low-conifer territories (Fig. 1a). Exactly opposite to their response to natural variation in habitat quality, jays showed no evidence for directional dispersal away from highways (Fig. 1b) but had lower survival rates on territories bordering highways compared to territories that did not border the highway (Fig. 1b). Thus, to our knowledge, we provide the first evidence that highways can act as a type of equal-preference ecological trap for animals.

Human-altered habitats are traditionally considered an ecological trap if animals use super-normal, maladaptive cues that attract them towards these areas (Schlaepfer et al. 2002). However, Robertson and Hutto (2006) recognized that there are situations where animals have lower fitness in altered habitats but show neutral preference between altered and natural habitats. Such equal-preference ecological traps could be quite common because, unlike super-normal traps, they don't require the development of a sensory exploitation mechanism. Equal-preference traps may be particularly relevant for forest-dependent species because they may perceive roads merely as natural gaps in the understory (e.g., Develey and Stouffer 2001; Norris and Stutchbury 2001; Mazerolle and Hobson 2003). We believe our results strongly support the idea that gray jays have a neutral preference towards high-mortality highway habitats because we first provided evidence that jays show directional dispersal in relation to natural variation in habitat quality and then demonstrated that the presence of a highway elicits no directional movement in either juveniles or adults.

Our dispersal results, along with previous work showing higher reproductive success on high-conifer territories (Strickland et al. 2011), also suggest that the proportion of conifers is a key feature that influences variation in territory quality in this species. A previous experiment suggested the mechanism that drives this relationship is the superior ability of coniferous trees to preserve cached food (Strickland et al. 2011), implying that gray jays occupying high-conifer territories have either a higher quantity or quality of cached food available throughout the winter. We suggest that suitable conifers not only drive variation in habitat quality at the population level but also play a significant role in determining the southern range limits of gray jays. In eastern North America mixed deciduous-coniferous forests found at the southern edge of the range likely result in biased dispersal towards conifer-dominated areas further north resulting in population sinks at the range

margins. In the west, sub-alpine Engelmann spruce *Picea engelmannii* forests support gray jays in the Rocky Mountains as far south as northern New Mexico and eastern Arizona but in the coastal ranges the spruce and the jays barely reach into northern California. To the south, in the Sierra Nevada, gray jays are absent from the high-altitude coniferous (but spruceless) forests although several other boreal species are present (Strickland and Ouellet 2011).

The fact that reproductive success, as shown in a previous study (Strickland et al. 2011), but not survival is related to habitat quality suggests that jays preferentially allocate resources towards self-maintenance (survival) over reproduction. This is perhaps somewhat surprising given that jays rely on perishable cached food during harsh and often unpredictable winters. Such conditions would seem to favor high reproductive output and result in low survival rates in the face of elevated and variable mortality rates during the winter. However, adults appear to have relatively high survival rates (~92 % survive the fall/winter, but see below) that are relatively constant over time, which suggests that they may allocate resources preferentially towards survival. Consistent with this type of life history strategy, they also have relatively low reproductive output (median clutch size: three; Strickland and Ouellet 2011) compared with other northern breeding birds, and they have never been observed to attempt second broods (Strickland and Ouellet 2011). Thus, it would seem that many life history characteristics of gray jays are closer to those of species living in less seasonal and lower latitude regions of the world that tend to allocate more resources towards survival rather than many species in other northern environments that are short-lived and have high reproductive output (e.g., Martin 1996; Ricklefs 1997; Boehning-Gaese et al. 2000; Sanz 2001; Cardillo 2002; Jetz et al. 2008).

Although we have shown that gray jays have higher survival rates during the fall/winter compared to the spring/summer, some caution is needed in interpreting seasonal differences in survival estimates because both adults and juveniles tend to disperse primarily in the summer when breeding vacancies more often become available. A further possible disincentive against winter dispersal is that jays must have enough time during the growing season to cache a sufficient amount of food on a new territory before the onset of winter. Although we have observed jays dispersing to new territories during fall/winter and surviving, it is often under these circumstances that pairs abandon or fail in their breeding attempts (D. S., D. R. N., unpublished data). Even more caution is needed for seasonal differences in juveniles because only one young from a brood typically remains with its parents beyond June, while the other young leave their natal territory at that time (Strickland 1991). Although we occasionally observe that some of

these early dispersing young are “adopted” by unrelated adults whose own nesting is usually observed to have failed (Strickland 1991; D. S., D. R. N., unpublished data), the vast majority are never observed on the study site again. This makes it impossible to distinguish directly between the proportion that die versus those that successfully disperse out of the study area to adoptive territories elsewhere. Nevertheless, although we do not yet have strong evidence that fall/winter survival is actually higher than spring/summer survival, our results do suggest that a reliance on cached food during the winter does not lead to elevated mortality rates, at least in adults.

Interestingly, despite the fact that this population has declined by over 50 % in the last 34 years, we found no evidence for a parallel temporal decline in survival rates. Previous work has reported negative trends in both clutch size and the proportion of successful nests (Waite and Strickland 2006). That reproduction is likely the vital rate driving the decline of this population is perhaps not surprising given that habitat quality, as measured by the proportion of conifers on territories, appears to influence reproduction but not survival. As we discussed above, our results point towards gray jays allocating limited resources to self-maintenance rather than reproduction, which implies that reproduction should be more sensitive to any potentially negative environmental effects.

As to what is causing declines, it is highly unlikely that changes in habitat quality have been a factor because our population is located along the main highway corridor for Algonquin Park, where the only significant environmental change in the last 70 years has been the ongoing, favorable-to-jays re-establishment of black spruce in lowland areas that were previously flooded as a result of logging activities in the late nineteenth and early twentieth centuries (Strickland 2003). Although, we have no information on the temporal changes in the amount of traffic through the park, it is unlikely that vehicle collisions with jays are causing declines because the declines are occurring in non-highway areas as well and no evidence exists that survival has changed over time. Waite and Strickland (2006) proposed that increasing fall temperatures were causing the decline in this population by spoiling cached food. We are currently examining this hypothesis and preliminary experimental evidence suggests a more complex relationship between cache quality and climate that involves freeze/thaw cycles and the duration of freezing, both of which have stronger temporal trends than fall temperatures. Once this is determined, we will examine how these climate variables influence survival, reproduction, and ultimately population growth rate.

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