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Supplemental feeding may reduce responsiveness of Black-capped Chickadees (*Poecile atricapillus*) to avian mobbing calls during gap-crossing experiments

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Abstract: Deforestation creates gaps in forest habitat, which can limit the movements of many avian species. Increased predation risk associated with crossing open habitats is often considered the primary impediment to crossing gaps. However, other factors such as energetic reserves may also influence these decisions. We conducted playback experiments before and after supplemental feeding of Black-capped Chickadees (*Poecile atricapillus* (Linnaeus, 1766)) to investigate how energetic reserves influenced gap-crossing decisions. Black-capped Chickadees were less likely to respond to playbacks, whether conducted within forests or across gaps, after supplemental feeding. This suggests that energetic reserves may have less influence on gap-crossing decisions than on the willingness of birds to respond to mobbing calls in general. We recommend that future studies investigating gap-crossing decisions using playbacks account for differences in resource availability among sampling locations, especially when making comparisons across discrete habitats.

Key words: Black-capped Chickadee, *Poecile atricapillus*, playback, gap-crossing decisions, energetic reserves, habitat fragmentation, movement.

Résumé : La déforestation crée des trouées dans les habitats forestiers qui peuvent limiter les déplacements de nombreuses espèces d'oiseaux. Le risque de prédation accru associé au franchissement d'habitats ouverts est souvent considéré comme étant le principal obstacle au franchissement de trouées. D'autres facteurs, tels que les réserves énergétiques, peuvent toutefois aussi influencer ces décisions. Nous avons mené des expériences de rediffusion de cris avant et après des supplémentations de nourriture données à des mésanges à tête noire (*Poecile atricapillus* (Linnaeus, 1766)) afin d'examiner l'influence des réserves énergétiques sur les décisions de franchissement de trouées. Les mésanges à tête noire étaient moins susceptibles de répondre à la rediffusion de cris, qu'elle soit effectuée dans la forêt et dans des trouées, après une supplémentation. Cela donne à penser que les réserves énergétiques pourraient exercer moins d'influence sur les décisions de franchissement de trouées que sur la volonté des oiseaux de répondre à des cris de houspillage en général. Nous recommandons que les études futures qui utilisent la rediffusion de cris pour examiner les décisions de franchissement de trouées tiennent compte des différences de disponibilité de ressources entre les lieux échantillonnés, en particulier lorsqu'il s'agit de comparer des habitats distincts. [Traduit par la Rédaction]

Mots-clés : mésange à tête noire, *Poecile atricapillus*, rediffusion de cris, décisions de franchissement de trouées, réserves énergétiques, fragmentation d'habitat, déplacement.

Introduction

Gaps in forest habitat resulting from fragmentation can affect movement behaviours across a range of taxa (Haddad 1999; Villard et al. 1999; Collinge 2000; Desrochers and Fortin 2000; Bélisle et al. 2001; Harris and Reed 2001; Ricketts 2001; Bakker and Van Vuren 2004; Riley et al. 2006; Duggan et al. 2012; Janin et al. 2012; Smith et al. 2013; Poessel et al. 2014). Limited movements of forest songbirds across these gaps created by fragmentation (Desrochers and Hannon 1997; Haddad 1999; Desrochers and Fortin 2000; Bélisle et al. 2001; Harris and Reed 2001; Bélisle and Desrochers 2002) can result in bird populations experiencing reduced connectivity between populations (Keller and Largiadèr 2003; Riley et al. 2006; Adams and Burg 2015) and decreased juvenile dispersal (Beauchamp et al. 1997; With et al. 1997). This could increase the vulnerability of threatened or sensitive species.

The reluctance of songbirds to cross forest gaps is often attributed to a perception of increased risk of predation from avian predators (e.g., hawks, falcons, and small owls) (Lima and Dill 1990; Rodríguez et al. 2001; Tellería et al. 2001; Desrochers et al. 2002). However, there is evidence that birds may consider factors other than predation risk when making gap-crossing decisions; ultimately, the decision of whether or not to cross a gap may result from a balance between these other competing pressures. For instance, energetic reserve levels may also play an important role for birds when making gap-crossing decisions. Turcotte and Desrochers (2003) demonstrated that birds in food-supplemented forest fragments were less likely to venture into gaps than those

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in non-supplemented fragments. They suggested that decreased energy stress, afforded by greater food access, reduced the energetic necessity to move in search of food and in turn made birds less likely to take risks associated with gap-crossings. Their finding suggests that birds who do cross habitat gaps may be engaging in a trade-off between foraging requirements and predation risk (Lima and Dill 1990; Walther and Gosler 2001).

The primary goal of our study was to investigate how supplemental feeding, as a proxy for energetic reserves, influences avian gap-crossing decisions. To test this, we conducted playback experiments before and after supplemental feeding during a concurrent study (Bailey et al. 2018) investigating the gap-crossing decisions of Black-capped Chickadees (*Poecile atricapillus* (Linnaeus, 1766)). We predicted that birds would be less likely to engage in risky behaviour, such as responding to mobbing calls broadcast from across a gap, if they occupied patches containing supplemental resources. We expected birds in these habitats to be less motivated to take risks, due to the higher resource availability provided by feeders. We also predicted that there would be little change in the likelihood of birds to respond to mobbing playbacks within continuous forest, even if supplemental feeders were available, because responding to these playbacks would not involve a gap-crossing. Responding to mobbing trials within continuous forest would not necessarily expose birds to elevated risk and therefore the trade-off between risk and resources would be less influential on their decisions.

Materials and methods

We conducted fieldwork for this study within Prince George, British Columbia, Canada (53.9049°N, 122.7667°W), between October 2016 and March 2017. Black-capped Chickadees are a species that is resident in the fall and winter months in British Columbia and they will readily use bird feeders (Foote et al. 2010). Gap-crossing behaviour of Black-capped Chickadees has been studied extensively using playback experiments (Desrochers and Hannon 1997; St. Clair et al. 1998; Desrochers and Fortin 2000; Bélisle et al. 2001; Bélisle and Desrochers 2002; Turcotte and Desrochers 2003; Groom 2006; Tremblay and St. Clair 2009; St-Louis et al. 2014; Adams and Burg 2015), making them a useful study species for our experiment.

We adapted our playback protocol from Tremblay and St. Clair (2009) so our results would be comparable with past studies (St. Clair 2003; Tremblay and St. Clair 2009). We conducted 22 playbacks at 11 different sites. Feeders were available at the different sites between 18 and 45 days (mean 23 days); as part of a parallel study (Bailey et al. 2018), feeders were established to band Black-capped Chickadees with passive integrated transponder (PIT) tags for radio frequency identification (RFID) tracking and the variation in feeder availability reflected the time required for flocks to find and consistently use feeders (approximately 4 to 20 days), band the birds at the site (approximately 5 to 7 days), then conduct 7-day RFID-tracking trials. The majority of the variance between sites was in the time required for flocks to initially locate and begin using feeders; once located, the mean number of days using feeders was more similar between sites. Sites were selected where a linear gap bisected forests, ranging in size from major walking trails (10–20 m), small to large forest service roads (30–50 m), through powerline transmission corridors (60–80 m). We selected an origin location in the forest on one side of the gap that served as the site of our starting playback. At each site, we conducted two types of playbacks: (1) playbacks where the origin and destination locations were on opposite sides of the gap (gap trials) and (2) playbacks where the origin and destinations were within continuous forest on the same side of, and running parallel to, the gap, i.e., did not require movement into open habitat (forest trials). At each site, we conducted both gap and forest playback trials prior to supplemental feeding and then again at the end of the feeding period. The playback distances at each site that we sampled were the same for the gap and forest trials, ranging from 17 to 80 m (distance was dictated by the size of the gap, as the origin location was in the forest on one edge of the gap and the destination location was in the edge of the forest on the immediate opposite side of the gap; an equivalent distance was used for playbacks in forest trials). We measured gap distances using a Bushnell Yardage Pro Sport 600 laser range finder. At each successive site, we alternated which trial type (gap or forest) was performed first.

Playback protocol

Each playback trial was conducted by two observers, one at the playback origin and the other at the playback destination. Each observer had a speaker (Logitech X100) connected to an iPod Touch that we used to broadcast a Black-capped Chickadee mobbing call. We placed each speaker roughly 1.5 m above the ground and positioned it pointing in the direction of the other observer. We standardized speaker volume across all trials (approximately 80 dB at 1 m) using a GoldLine SPL120 sound pressure meter. We chose this volume because it is similar to natural calling and because it was sufficiently loud to be audible to the second observer at all distances that we sampled.

We began each playback with a 30 s primer of Black-capped Chickadee mobbing calls at the origin location, followed by 1 min of silence. Next, we began playing the same mobbing call at the origin location for up to a maximum of 6 min, or until no new birds had arrived for 1 min. If no birds responded after the first 2 min of the 6 min playback, then we stopped the playback for 2 min and restarted the trial. We repeated this protocol until birds either began responding to the playback, or the entire 6 min playback had elapsed with no birds responding (in the latter case, the trials were aborted until the next day; see below). For a playback trial at the origin location to proceed to testing at the destination location, at least one bird had to have been attracted to within 10 m of the origin speaker and indicate some form of responsiveness to the mobbing call (i.e., calling or approaching the speaker). Once these conditions had been met, the observer at the origin turned their speaker off and moved to a location halfway between the origin and the destination speakers to observe and record birds moving from the initial location to the destination speaker. Simultaneously, the observer at the destination speaker began their mobbing call playback. We broadcasted the mobbing call for 6 min continuously at the destination location. Our criterion for a bird to successfully respond to the destination call was the same as those used at the origin location. After the first playback type (gap or forest trial) was completed, we conducted the reciprocal trial immediately (typically within 1–5 min). If only one or neither of the gap or forest playback trials was successful in attracting birds to the origin location, then we aborted the playback and attempted it again the following day. For successful playbacks, we recorded the number of birds at the initial location and the number of individuals that moved to the destination location; we used this as the dependent variable in our models.

Statistical analysis

We performed all statistical analyses using STATA version 14 (StataCorp LLC 2015). To analyze the responses of birds to our playbacks, we constructed mixed-effects logistic regression models with binomial distributions and logit link functions. We used the number of birds at the destination location (i.e., number of bird that moved in response to playback) as our dependent variable and the number of birds at the origin location (i.e., total number of bird responding to the initial playback) as a binomial denominator. Therefore, for a single playback trial, each individual bird that approached the origin location was scored as either successfully (1) or unsuccessfully (0) moving to the destination location. To account for the potential for other birds to influence

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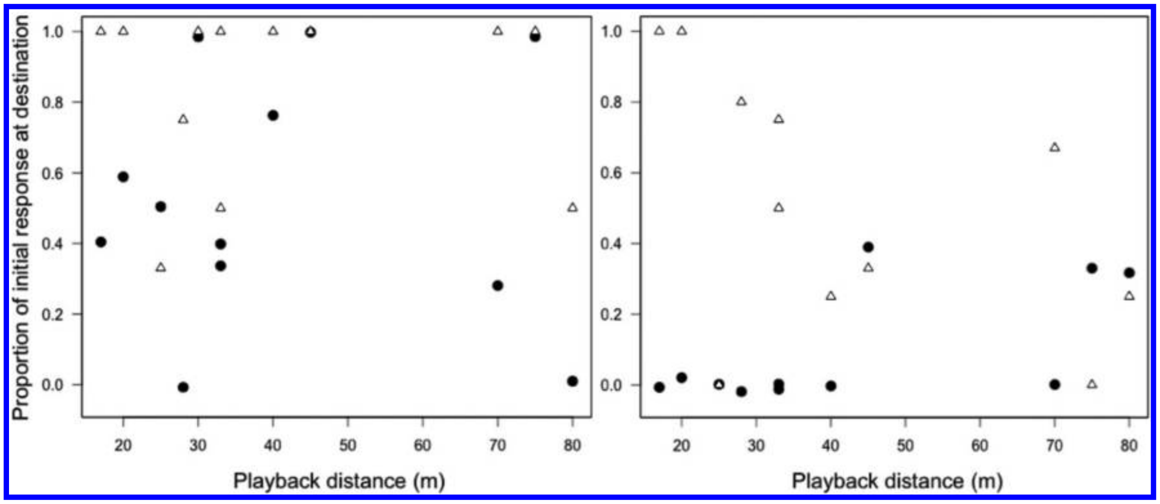
Fig. 1. The proportion of responses to destination playbacks across all playback distances for gap (circles) and forest (triangles) trials both before feeding (left) and after feeding (right). After-feeding trials had much lower responses overall compared with before-feeding trials; however, in the after-feeding trials, a few responses at large distances likely skewed our results to show a positive interaction between gap-trial playback responses and increased gap distance. Graphed data points are jittered to better illustrate overlapping points.



gap-crossing decisions of individuals, we included the total number of birds responding to the origin-location playback in each individual playback as the binomial denominator (herein referred to as the "response proportion"). This then uses the total number of playbacks, rather than the total number of responding birds, as our sample size for analysis. All of our models included a random intercept for site to account for the two types of trials (gap trials and forest trials) being performed at the same sites.

To confirm assumptions that trial order (i.e., whether the first trial at a site was a gap playback or a forest playback) at a site did not impact the overall responsiveness of birds to playbacks, we used the response proportion for each trial as the dependent variable and the trial type that was performed first at that site as a categorical predictor variable (forest trial = 0; gap trial = 1). If trial order was not found to affect response, we subsequently removed this from further analysis.

To investigate how supplemental feeding influenced gap-crossing behaviours, we tested if playback responses differed before vs. after food supplementation. To test this, we used the response proportion as the dependent variable and whether the trial was performed before feeding or after feeding as a categorical predictor variable (before feeding = 0; after feeding = 1). To test if this effect was only present during gap or forest trials, we partitioned the data into gap trials and forest trials and again tested response proportion as the dependent variable and whether the trial was performed before feeding or after feeding as a categorical predictor variable on both data sets. We also included number of supplemental feeding days as a continuous predictor variable for the after-feeding trials to see if differences in duration of food supplementation influenced playback responses.

To ask whether gaps in forest habitat negatively impacted bird movements, we used the response proportion as the dependent variable, the trial type as a categorical predictor variable (forest trial = 0; gap trial = 1), and the playback distance as a continuous predictor variable. We looked at the interaction between playback type and distance because we suspected the effect of distance on response proportion may only be evident during gap trials. In this model, we used the response proportion as the dependent variable, trial type and playback distance as predictor variables, and included a trial type × playback distance interaction term. To further investigate significant interactions between trial type and playback distance, we used the response proportion as the dependent variable and playback distance as a continuous predictor variable for both gap trials and forest trials separately.

Animal care approval

This research was approved by the University of Northern British Columbia's Animal Care and Use Committee (protocol No. 2014-6) and follows the guidelines of both the Association for the Study of Animal Behaviour and the Canadian Council on Animal Care.

Results

The likelihood of birds responding to a playback was not influenced by which trial (gap or forest) we performed first (Wald χ^2 = 0.06, n = 44, P = 0.81), so we did not use playback order as a random effect in subsequent models. Birds were significantly less likely to respond to our destination speaker mobbing playbacks during the after-feeding playback trials compared with the before-feeding playback trials. This was true when we analyzed all trials together (Wald χ^2 = 16.27, n = 44, P = 0.0001) and when we partitioned the data into gap trials (Wald χ^2 = 10.77, n = 22, P = 0.001) and forest trials (Wald χ^2 = 8.50, n = 22, P = 0.004; Fig. 1) separately.

For our before-feeding trials, we found no significant interaction between playback distance and trial type (gap trials vs. forest trials) (P = 0.72). We therefore dropped the nonsignificant interaction to derive our final model. The full model including trial type and playback distance was significant (Wald χ^2 = 10.70, n = 22, P = 0.004), so we investigated the contributions of the variables to the model. Increased playback distance did not influence the proportion of birds that responded to our playbacks (β = 0.003, z = 0.12, P = 0.90). During the before-feeding trials, however, birds were significantly less likely to respond to mobbing playback when doing so involved a gap-crossing (gap trials) than when they did not (forest trials) (β = –2.12, z = –3.27, P = 0.001).

The final model for after-feeding playback trials including the number of feeding days, playback distance, trial type, and the interaction between trial type and playback distance was significant (Wald χ^2 = 11.67, n = 22, P = 0.02). The number of feeding days had no influence on playback response probability (β = 0.037, z = 0.84, P = 0.40), whereas distance between the origin speaker and the destination speaker had a moderate negative effect on response (β = –0.03, z = –1.70, P = 0.09). Again, birds were also significantly less likely to respond to gap-trial playbacks compared with forest-trial playbacks (β = –5.87, z = –2.97, P = 0.003), but there was also a significant positive interaction between distance and trial type (β = 0.08, z = 2.33, P = 0.02; Fig. 1). This interaction suggests that birds were more likely to respond to gap-trial playbacks as distance increased. However, when we investigated this interac-

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tion further, playback distance on its own had no significant effect on response probability during the after-feeding gap trials (Wald $\chi^2 = 2.08$, $n = 11$, $P = 0.15$) or the after-feeding forest trials (Wald $\chi^2 = 2.25$, $n = 11$, $P = 0.13$).

Discussion

Black-capped Chickadees were significantly less likely to respond to mobbing playbacks where the destination speaker involved crossing forest gaps compared with those where the destination speaker was within the same forest patch. This supports the findings from previous studies, which showed that gaps act as barriers to movement (Desrochers and Hannon 1997; St. Clair et al. 1998; Desrochers and Fortin 2000; Bélisle et al. 2001; Bélisle and Desrochers 2002; Turcotte and Desrochers 2003; Groom 2006; Tremblay and St. Clair 2009; St-Louis et al. 2014; Adams and Burg 2015). However, perhaps the most interesting result of our study was the overall decrease in responsiveness to approaching mobbing playbacks between our before-feeding trials and our after-feeding trials, as this decrease was seen in both our gap trials and our forest trials. Because our before-feeding and after-feeding trials were separated by at least 18 days, habituation to playbacks is unlikely to explain the reduction in mobbing response. Also, because birds were less likely to respond after feeding regardless of which trial type (gap or forest) was preformed first, this also suggests that the reduction in after-feeding responses was related to the food supplementation and not habituation to the mobbing call. One possibility is that food supplementation may have diminished the risk-taking propensity of birds not just to gap-crossing, but to mobbing in general. Because mobbing is a risky behaviour (Sordahl 1990), birds may have been less motivated to respond to mobbing calls as the stimulus moved from the origin speaker to the destination speaker. Birds may have perceived the "predator" as having moved away as the stimulus shifted to the destination speaker and thus was no longer potentially hampering access to a perceived food source near the origin speaker. As a localized food source might reduce the total area the birds need to travel, they may simply have chosen not to venture to the destination feeder to pursue the predator, regardless of whether or not this involved a gap-crossing.

During our sampling period, the feeders that we used to supplement birds were also outfitted with RFID readers and many birds in our study population were banded with PIT tags as part of a concurrent study (Bailey et al. 2018). Results from the RFID-tracking study found that gaps in our study area do appear to impede Black-capped Chickadee movements. When using RFID feeders to track movement, the prime impediment to interfeeder movement was when these involved crossing a gap, which was exacerbated by the increasing gap size (Bailey et al. 2018). However, during RFID tracking, food supplementation did not influence bird movements within forests or across gaps. This finding is in stark contrast to the overall decrease in responses to mobbing playbacks after feeding in the current study. Movements recorded between feeder visitations in Bailey et al. (2018) were recorded by tracking birds over multiple days, though, as opposed to short-term movements invoked via mobbing playbacks in the current study. In conjunction, these findings suggest that resource availability may have less influence on reducing gap-crossings than it does on responding to mobbing calls. However, as we were constrained by a relativity small sample size for our playback experiments, more work is needed to investigate the influence of resource availability and bird energetic reserves on mobbing responses, specifically as they relate to use of mobbing calls in playback studies.

Our playback results run somewhat contrary to other playback studies; whereas others found that increased gap distance imposed a greater impediment to movement (Desrochers and Hannon 1997; Rodríguez et al. 2001; Harris and Reed 2001; Bélisle and Desrochers 2002; Tremblay and St. Clair 2009), our study did not find this effect of gap distance. This may result from the smaller gap distances used in our study (17–80 m) compared with those of others (e.g., up to 160 m) (i.e., Desrochers and Hannon 1997). Had we been able to sample larger gap distances, differences in response probability may have been more pronounced, but gaps of this size are not common in the hydro and forestry right of ways used in our research. RFID tracking, though, did find that movements between feeders were reduced between even these small gap distances (Bailey et al. 2018).

When we analyzed the after-feeding playback trials alone, we found birds appeared more likely to respond to mobbing calls during gap-trial playbacks as gap distance increased. This unexpected result was present for our after-feeding playback trials only. However, this interaction appears to be due to a few outlier responses where birds responded to our playbacks at higher rates than would be expected at large gap distances, rather than an overall trend of increasing responses with increased gap distance (Fig. 1).

We recommend future studies looking at the effects of habitat fragmentation using mobbing call playbacks take into account differences in resource availability among sampling locations, especially when comparing responses across different habitats. Birds in areas of differing resource availabilities may differ in their propensities to respond to mobbing calls. If the goal of a study is to compare responses across habitats, then differences in resources may obscure results obtained through use of mobbing call playbacks.

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References

Adams, R.V., and Burg, T.M. 2015. Gene flow of a forest-dependent bird across a fragmented landscape. PLoS ONE, **10**: e0140938. doi:10.1371/journal.pone.0140938. PMID:26580222.

Bailey, J.M., Reudink, M.W., LaZerte, S.E., Paetkau, M., Johnson, C.J., Hill, D.J., and Otter, K.A. 2018. Using radio frequency identification (RFID) to investigate the gap-crossing decisions of Black-capped Chickadees (*Poecile atricapillus*). Auk, **135**(3): 449–460. doi:10.1642/AUK-17-162.1.

Bakker, V.J., and Van Vuren, D.H. 2004. Gap-crossing decisions by the red squirrel, a forest-dependent small mammal. Conserv. Biol. **18**(3): 689–697. doi:10.1111/j.1523-1739.2004.00149.x.

Beauchamp, G., Belisle, M., and Giraldeau, L.A. 1997. Influence of conspecific attraction on the spatial distribution of learning foragers in a patchy habitat. J. Anim. Ecol. **66**(5): 671–682. doi:10.2307/5920.

Bélisle, M., and Desrochers, A. 2002. Gap-crossing decisions by forest birds: an empirical basis for parameterizing spatially-explicit, individual-based models. Landsc. Ecol. **17**(3): 219–231. doi:10.1023/A:1020260326889.

Bélisle, M., Desrochers, A., and Fortin, M.J. 2001. Influence of forest cover on the movements of forest birds: a homing experiment. Ecology, **82**(7): 1893–1904. doi:10.2307/2680055.

Collinge, S.K. 2000. Effects of grassland fragmentation on insect species loss, colonization, and movement patterns. Ecology, **81**(8): 2211–2226. doi:10.1890/0012-9658(2000)081[2211:EOGFOI]2.0.CO;2.

Desrochers, A., and Fortin, M.J. 2000. Understanding avian responses to forest boundaries: a case study with chickadee winter flocks. Oikos, **91**(2): 376–384. doi:10.1034/j.1600-0706.2000.910218.x.

Desrochers, A., and Hannon, S.J. 1997. Gap crossing decisions by forest songbirds during the post-fledging period. Conserv. Biol. **11**(5): 1204–1210. doi:10.1046/j.1523-1739.1997.96187.x.

Desrochers, A., Bélisle, M., and Bourque, J. 2002. Do mobbing calls affect the perception of predation risk by forest birds? Anim. Behav. **64**(5): 709–714. doi:10.1006/anbe.2002.4013.

Duggan, J.M., Heske, E.J., and Schooley, R.L. 2012. Gap-crossing decisions by adult Franklin's ground squirrels in agricultural landscapes. J. Mammal. **93**(5): 1231–1239. doi:10.1644/11-MAMM-A-418.1.

Foote, J.R., Mennill, D.J., Ratcliffe, L.M., and Smith, S.M. 2010. Black-capped Chickadee (*Poecile atricapillus*), version 2.0. *In* The birds of North America. *Edited by* A.F. Poole. Cornell Lab of Ornithology, Ithaca, N.Y. doi:10.2173/bna.39.

Groom, J.D. 2006. Patch colonization dynamics in Carolina Chickadees (*Poecile carolinensis*) in a fragmented landscape: a manipulative study. Auk, **123**(4): 1149–1160. doi:10.1642/0004-8038(2006)123[1149:PCDICC]2.0.CO;2.

Haddad, N.M. 1999. Corridor use predicted from behaviors at habitat boundaries. Am. Nat. **153**(2): 215–227. doi:10.1086/303163. PMID:29578761.

Harris, R.J., and Reed, J.M. 2001. Territorial movements of Black-throated Blue Warblers in a landscape fragmented by forestry. Auk, **118**(2): 544–549. doi:10.1642/0004-8038(2001)118[0544:TMOBTB]2.0.CO;2.

Janin, A., Léna, J.P., and Joly, P. 2012. Habitat fragmentation affects movement behavior of migrating juvenile common toads. Behav. Ecol. Sociobiol. **66**(9): 1351–1356. doi:10.1007/s00265-012-1390-8.

Keller, I., and Largiadèr, C.R. 2003. Recent habitat fragmentation caused by major roads leads to reduction of gene flow and loss of genetic variability in ground beetles. Proc. R. Soc. B Biol. Sci. **270**(1513): 417–423. doi:10.1098/rspb.2002.2247.

Lima, S.L., and Dill, L.M. 1990. Behavioral decisions made under the risk of predation: a review and prospectus. Can. J. Zool. **68**(4): 619–640. doi:10.1139/z90-092.

Poessel, S.A., Burdett, C.L., Boydston, E.E., Lyren, L.M., Alonso, R.S., Fisher, R.N., and Crooks, K.R. 2014. Roads influence movement and home ranges of a fragmentation-sensitive carnivore, the bobcat, in an urban landscape. Biol. Conserv. **180**: 224–232. doi:10.1016/j.biocon.2014.10.010.

Ricketts, T.H. 2001. The matrix matters: effective isolation in fragmented landscapes. Am. Nat. **158**(1): 87–99. doi:10.1086/320863. PMID:18707317.

Riley, S.P.D., Pollinger, J.P., Sauvajot, R.M., York, E.C., Bromley, C., Fuller, T.K., and Wayne, R.K. 2006. A southern California freeway is a physical and social barrier to gene flow in carnivores: physical and social barrier to gene flow. Mol. Ecol. **15**(7): 1733–1741. doi:10.1111/j.1365-294X.2006.02907.x. PMID:16689893.

Rodríguez, A., Andrén, H., and Jansson, G. 2001. Habitat-mediated predation risk and decision making of small birds at forest edges. Oikos, **95**(3): 383–396. doi:10.1034/j.1600-0706.2001.950303.x.

Smith, M.J., Forbes, G.J., and Betts, M.G. 2013. Landscape configuration influences gap-crossing decisions of northern flying squirrel (*Glaucomys sabrinus*). Biol. Conserv. **168**: 176–183. doi:10.1016/j.biocon.2013.10.008.

Sordahl, T.A. 1990. The risks of avian mobbing and distraction behavior: an anecdotal review. Wilson Bull. **102**(2): 349–352.

StataCorp LLC. 2015. STATA. Version 14. StataCorp LLC, College Station, Tex.

St. Clair, C.C. 2003. Comparative permeability of roads, rivers, and meadows to songbirds in Banff National Park. Conserv. Biol. **17**(4): 1151–1160. doi:10.1046/j.1523-1739.2003.02156.x.

St. Clair, C.C., Bélisle, M., Desrochers, A., and Hannon, S. 1998. Winter responses of forest birds to habitat corridors and gaps. Conserv. Ecol. **2**(2): 13. Available from http://www.consecol.org/vol2/iss2/art13/.

St-Louis, V., Forester, J.D., Pelletier, D., Bélisle, M., Desrochers, A., Rayfield, B., Wulder, M.A., and Cardille, J.A. 2014. Circuit theory emphasizes the importance of edge-crossing decisions in dispersal-scale movements of a forest passerine. Landsc. Ecol. **29**(5): 831–841. doi:10.1007/s10980-014-0019-x.

Tellería, J.L., Virgós, E., Carbonell, R., Pérez-Tris, J., and Santos, T. 2001. Behavioural responses to changing landscapes: flock structure and anti-predator strategies of tits wintering in fragmented forests. Oikos, **95**(2): 253–264. doi:10.1034/j.1600-0706.2001.950207.x.

Tremblay, M.A., and St. Clair, C.C. 2009. Factors affecting the permeability of transportation and riparian corridors to the movements of songbirds in an urban landscape. J. Appl. Ecol. **46**(6): 1314–1322. doi:10.1111/j.1365-2664.2009.01717.x.

Turcotte, Y., and Desrochers, A. 2003. Landscape-dependent response to predation risk by forest birds. Oikos, **100**(3): 614–618. doi:10.1034/j.1600-0706.2003.12234.x.

Villard, M.A., Trzcinski, M.K., and Merriam, G. 1999. Fragmentation effects on forest birds: relative influence of woodland cover and configuration on landscape occupancy. Conserv. Biol. **13**(4): 774–783. doi:10.1046/j.1523-1739.1999.98059.x.

Walther, B., and Gosler, A. 2001. The effects of food availability and distance to protective cover on the winter foraging behaviour of tits (Aves: *Parus*). Oecologia, **129**: 312–320. doi:10.1007/s004420100713. PMID:28547610.

With, K.A., Gardner, R.H., and Turner, M.G. 1997. Landscape connectivity and population distributions in heterogeneous environments. Oikos, **78**(1): 151–169. doi:10.2307/3545811.

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