

The cost of dispersal: predation as a function of movement and site familiarity in ruffed grouse

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Ecologists often assume that dispersing individuals experience increased predation risk owing to increased exposure to predators while moving. To test the hypothesis that predation risk is a function of movement distance or rate of movement, we used radio-telemetry data collected from 193 ruffed grouse (*Bonasa umbellus*) during 1996–1999 in southeastern Ohio. Cox's proportional hazards model was used to examine whether the risk of predation was affected by the rate of movement and site familiarity. We found evidence indicating that increased movement rates may increase the risk of predation for adult birds but not juveniles. We also found juvenile and adult birds inhabiting unfamiliar space were consistently at a much higher risk of predation (three to 7.5 times greater) than those in familiar space. Our results indicate that although movement itself may have some effect on the risk of being preyed upon, moving through unfamiliar space has a much greater effect on risk for ruffed grouse. This supports the hypothesis that increased predation risk may be an important cost of dispersal for birds. *Key words*: Cox's proportional hazards model, dispersal cost, movement rate, predation risk, ruffed grouse, site familiarity. [*Behav Ecol* 15:469–476 (2004)]

Determining the costs of dispersal is crucial to understanding the evolutionary causes of dispersal (Johnson and Gaines, 1990) and their demographic consequences (Bélíchon et al., 1996). There has been widespread speculation by ecologists that dispersers experience higher mortality risk and lower reproductive success than do philopatric individuals (see Anderson, 1989; Gaines and McClenaghan, 1980; Jones, 1988; Lidicker, 1975). Dispersal-related mortality may be owing to increased predation pressure, aggression, stress, energy depletion, or moving through or settling in unfamiliar areas (Greenwood and Harvey, 1982; Van Vuren and Armitage, 1994). Dispersers may also incur costs associated with investments in morphology necessary for successful dispersal (Dieckmann et al., 1999), such as trade-offs between flight capability and reproduction in many wing-polymorphic insect species (Langellotto et al., 2000).

Predation is often assumed to be the cause of differences in survival between dispersers and philopatric individuals (Gaines and McClenaghan, 1980). Predation risk may be greater for dispersers than for nondispersers because of (1) greater activity rates, (2) lower familiarity with new habitats, or (3) use of lower-quality habitat by dispersers. Movement of dispersing individuals may attract the attention of predators. The energetic demands of movement may also affect a disperser's ability to avoid or deter predators or may cause a disperser to forage at risky times. It is well established that an increase in the threat of predation can result in a decrease in prey activity such as nest or den building or daily foraging (Lima, 1998; Lima and Dill, 1990). A common assumption across taxa is that increased activity itself can cause an increase in predation risk, although this is only rarely supported by

direct evidence (for reviews, see Gaines and McClenaghan, 1980; Johnson and Gaines, 1990). Higher predation rates of more active individuals have been found in kangaroo rats (Daly et al., 1990), field and sibling voles (Norrdahl and Korpimäki, 1998), wood frogs (Skelly, 1994), and various fish and invertebrates (for references, see Lima, 1998).

Individuals undergoing natal or breeding dispersal move through and inhabit unfamiliar space. They may have little knowledge of where to find food in the area (resulting in low energetic efficiency) or where to find cover from predators (Clarke et al., 1993; Jacquot and Solomon, 1997). Whereas the effects of high activity rate would be important only during the actual movement phase of dispersal (transience), the effects of unfamiliar space may be important both during transience and after settlement in a new territory. The effects of energy depletion from increased activity or from foraging inefficiency in an unfamiliar area may be important both during dispersal and after settlement.

Previous studies have attempted to compare survival rates of philopatric and dispersing individuals, both during transience and after settlement. A review of 10 studies of birds (two studies) and mammals (eight studies) comparing disperser survival during transience to survival during the same period for philopatric individuals showed dispersers to have lower survival (Bélíchon et al., 1996). However, these studies were biased toward the use of mark–recapture techniques, which may give misleading estimates of survival for long-range dispersers, (see Discussion). In a review of 19 studies comparing survival after settlement, there was no consistent difference in survival between dispersers and philopatric individuals (Bélíchon et al., 1996). Studies comparing survival after settlement have limited ability to address the question of whether an increase in mortality owing to predation is at least partially owing to movement per se (i.e., activity itself making dispersers vulnerable to predators). Many of these studies compare survival rates of individuals born on a particular site with survival of those thought to have immigrated to that site, and thus, these studies fail to measure predation during the transient phase. Because comparisons are made after dispersal is completed, differences in survival between dispersers and nondispersers

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can be owing to the effects of unfamiliar space or energy depletion from the dispersal period, but will not be owing to activity itself making dispersers vulnerable to predators.

Most previous survival analyses (telemetry or mark recapture) are also limited by the fact that each individual must be classified as being either a disperser or philopatric. Because there are almost as many different ways of defining a disperser as there are studies and species, comparisons between studies are difficult. Almost all methods include some arbitrary decisions about minimum distance moved when defining dispersal, and these may bias the analysis. Bias is most likely to occur when classifying individuals that have died at the beginning of the transient phase. Because it is impossible to determine how far an individual would have moved if it had not been killed, some individuals are never classified as having dispersed but may have still been killed owing to the effects of high activity rates.

Relating predation events to distance moved or rate of movement would provide direct estimates of the predation-related survival cost to dispersers and could be calculated during both transience and settlement phases. The use of such a quantitative measure would also avoid some of the methodological concerns in the analysis of survival estimates.

The objective of the present study was to use measurements of radio-collared ruffed grouse (*Bonasa umbellus*) to test the hypothesis that predation risk increases with rate of movement. We also attempted to differentiate the effects of movement per se and residing in unfamiliar space on predation risk. We modeled mortality owing to predation as a function of an individual's rate of movement before predation events and included in the models the effect of inhabiting familiar versus unfamiliar space at the time of a predation event. We also separately modeled the effect of rate of movement and site familiarity on the mortality risk owing exclusively to avian predators, mammalian predators, and hunting.

METHODS

Study species

The ruffed grouse is a nonmigratory, forest game bird. In general, it undertakes significant dispersal movements during the fall (Bump et al., 1947; Small and Rusch, 1991) and primarily between 1 October and 1 December in Ohio (Yoder, 1998). Approximately 80% of juvenile birds undertake some form of natal dispersal after brood break-up in mid-September. Some adult birds (approximately 20–30%) also undergo large-scale movements during this time as they move between spring/summer and winter ranges (Yoder, 1998). Daily movement distances can range from less than 100 m to more than 2 km, whereas net seasonal distances can range from a few hundred meters to more than 14 km (Yoder, 1998). The mean length of a dispersal, or transient, period for an individual bird is approximately 2 weeks (Yoder, 1998).

Study sites

The study was conducted at two sites in southeastern and east central Ohio from 1996–1999. The sites were centered on Waterloo Wildlife Area in Athens County and Woodbury Wildlife Area in Coshocton County. Each study site included the state-owned wildlife area and surrounding private lands within 15 km. The sites were characterized by a mixture of early successional to 40+-year-old oak-hickory forest and agricultural fields.

Each fall, from 1 August–10 October, 35–50 birds were trapped at each site by using modified lily-pad traps (Dorney and Mattison, 1956). Radio transmitters (Advanced Telemetry

Systems) were attached with a necklace harness (Amstrup, 1980) of Teflon-coated woven wire. Mean transmitter weight was 11 g. Only birds weighing more than 250 g were fitted with transmitters to ensure that the transmitter was 5% or less of the bird's body weight (Fuller, 1987). Expected battery life of transmitters was 320–500 days. Transmitters were distributed as equally among all age-sex categories as possible (approximately 55% adult and 45% juveniles, 57% males and 43% females). In all, a total of 193 birds were tagged and tracked over the course of 3 years.

Movement data

Attempts were made to locate all tagged birds at least three or four times per week from 1 August 1–15 May and at least biweekly during June and July. Individual locations were calculated by using the maximum likelihood estimator method (Lenth, 1981) with a minimum of three azimuths taken within a span of 10 min. Lenth's method generates a 95% error ellipse of the bird's location. Only locations with 95% error ellipses smaller than 2 ha were used in distance calculations (92% of all locations). To calculate average daily rate of movement, we used the total distance moved during a given time interval (calculated by summing distances between each successive pair of locations during the given interval) divided by the total number of days in that interval.

All transmitters were equipped with mortality-mode switches (i.e., when the transmitter remains stationary for 6–8 h, the pulse rate doubles). This allowed for quick location and recovery of dead birds. After necropsy, all recovered birds were classified as killed by avian, mammalian, or unknown predators, or as dying by other causes (e.g., road kill; Einarsen, 1956; Dumke and Pils, 1973). In addition, each bird was equipped with a reward leg band that facilitated the identification of birds harvested during the hunting season (10 Oct–29 Feb). Over the 3-year study, the fate of 13% of tagged birds was unknown, most likely owing to transmitter failure. To avoid any effect of short-term stress owing to capture and handling or from transmitters, birds that died within 7 days of capture were not included in the analyses.

Data analysis

If the risk of predation increases with movement distance or rate of movement, then movement rate should have a significant effect on bird survival. Because predation risk and movement rates vary over time, we wanted to assess the effect of the rate of movement at the time of each predation event on the predation risk for all birds in the study. To accomplish this, we used a method of survival analysis based on the extended Cox's proportional hazards model (Hougaard, 2000; Kleinbaum, 1996; White and Garrott, 1990). Although this semiparametric model has been used only rarely in ecological studies, it is popular in clinical studies in the health sciences. The model estimates the hazard (i.e., the effect on survival time) for an individual owing to one or more explanatory covariates. A particularly powerful characteristic of this model is its ability to handle both time-independent and time-dependent individual covariates.

General model description

The basic hazard model used in our analyses is expressed as:

$$h(t) = h_0(t) \exp(\beta_1 \text{SEX} + \beta_2 \text{STUDYAREA} + \beta_3 \text{YEAR} + \delta_2 \text{SITE}(t) + \delta_1 \text{RATE}(t)) \quad (1)$$

where the hazard function (h) for an individual at time t is a function of the baseline hazard function (h_0) and the

covariates are SEX, STUDY AREA, YEAR (study year), RATE (the movement rate of each individual expressed in minutes per day at time t), and SITE (familiar or unfamiliar space at time t). Time t is measured as the time (in days) since the start of the trapping period (1 August) each year. The hazard function (h_0) is considered the starting (or “baseline”) version of the hazard function in that the formula reduces to this function if no covariates are included in the model (or all covariates = 0). The regression coefficients β_{1-3} and δ_{1-2} measure the degree to which each covariate in the model affects mortality owing to predation. In our model the covariates SEX, STUDY AREA, and YEAR are time independent. Movement rate (RATE) and site familiarity (SITE) may change over time, and because this is owing to behavior specific to an individual, they are termed “internal” time-dependent covariates (Kleinbaum, 1996). Although the value of the covariate RATE changes over time, there is only a single coefficient (δ_1) for the time-dependent covariate in the model. Thus, the effect of the time-dependent variable RATE on the hazard at time t is based only on one value of RATE, the value being measured at time t . In practice, this means that a new movement rate was calculated for each individual bird in the study at each time t of interest, in this case, the date of each predation event. Likewise, the status of SITE for each bird was also updated on the date of each predation event.

We performed the analysis by using PROC PHREG in SAS (SAS 8.1). PROC PHREG estimates regression coefficients for the hazard function by using a partial likelihood function that considers probabilities only for those subjects preyed upon during the course of the study. All birds who are alive and for which we have data for a given day in the model make up the “risk set” for each predation event.

PROC PHREG estimates a hazard ratio for each covariate. The hazard ratio describes the relative risk between values of an individual covariate. If the hazard ratio is larger than one, then an increment increase in the variable causes an increase in the risk of predation. A hazard ratio less than one signifies a decrease in the risk of predation. For example, the hazard ratio for the SEX covariate in our model is a measure of the relative predation risk of males versus females. Because males were coded as one and females as two in our analysis, a hazard ratio greater than one would indicate females experience an overall higher predation risk than do males. When evaluating the relative risks for internal time-dependent variables, a slightly different interpretation of the hazard ratio is necessary. The variable RATE in our model is not distinguishing the relative risk between two separate groups (e.g., males versus females) but is estimating the relative risk only at any given time t for an individual moving at some rate r compared with an individual moving at a rate of $r + 1$ minutes per day (Kleinbaum, 1996). The hazard ratio for the variable SITE estimates the relative risk at any given time t of inhabiting familiar versus unfamiliar space.

If a regression coefficient is significantly different from zero, then a hazard ratio can be used to estimate the effect of that variable on predation risk. PROC PHREG uses the Wald statistic, which has a chi-square distribution, to determine if estimated regression coefficients are significantly different from zero.

Because overall annual survival rates (S) estimated with likelihood models using program MARK were significantly different for hatch-year birds (juveniles; $S = 0.273$, $SE = 0.039$) and after-hatch-year birds (adults; $S = 0.469$, $SE = 0.38$) (Swanson DA, unpublished data), we performed separate analyses for juveniles and adults. There was no evidence for significant differences in overall seasonal survival rates, with mortality spread evenly throughout the year. The origin point

for an individual’s survival time was 1 August of each year, and we assumed that adult annual mortality was independent of age.

Because it is not clear exactly which time period of movement might be most important in determining predation rate, we ran three different models for each age class, all of which included SEX, STUDY AREA, YEAR, SITE, and RATE but differed in the period of time over which movements were used to calculate the time-dependent variable RATE. Each time period ended with the same date (at a predation event t) but had different initial dates. The three initial dates used were an individual’s capture and tagging date, the date 14 days before the predation event, and the date of the individual’s penultimate location (if it was located within 3 days of the predation event.) Thus, our analysis of the effect of movement rates on predation risk included a set of three models for both juveniles and adults:

$$h_c(t) = h_{0,c}(t) \exp(\beta_1 \text{SEX} + \beta_2 \text{STUDYAREA} + \beta_3 \text{YEAR} + \delta_2 \text{SITE}(t) + \delta_1 \text{RATE}_{\text{capture}}(t)) \quad (2)$$

$$h_{14}(t) = h_{0,14}(t) \exp(\beta_1 \text{SEX} + \beta_2 \text{STUDYAREA} + \beta_3 \text{YEAR} + \delta_2 \text{SITE}(t) + \delta_1 \text{RATE}_{14\text{day}}(t)) \quad (3)$$

$$h_3(t) = h_{0,3}(t) \exp(\beta_1 \text{SEX} + \beta_2 \text{STUDYAREA} + \beta_3 \text{YEAR} + \delta_2 \text{SITE}(t) + \delta_1 \text{RATE}_{3\text{day}}(t)) \quad (4)$$

where $\text{RATE}_{\text{capture}}$ is the movement rate calculated over the period ($t - \text{capture date}$) to t , $\text{RATE}_{14\text{day}}$ is the movement rate calculated over the period ($t - 14$) to t , and $\text{RATE}_{3\text{day}}$ is the movement rate calculated over the period ($t - 3$) to t .

To investigate the effect of site familiarity on predation risk, we included the time-dependent binomial variable SITE that varied according to the familiarity of the area inhabited by an individual at the time of a predation event. At any given predation event (t), an individual was classified as inhabiting familiar space if it was previously located within 500 m of that location during any point in its life prior to 14 days before t . Conversely, an individual was in unfamiliar space if it had never been located within 500 m of its current locations before the last 2 weeks. This definition of familiar space is somewhat arbitrary; however, a distance of 500 m is based on a mean home range size for grouse in our study (during nondispersing periods) of 46 ha (Yoder JM, unpublished data), which corresponds to a circular area with a radius of 380 m. Therefore, we believe if an individual bird is found to be greater than 500 m from any previous location, it is highly likely that it is currently in an unfamiliar area. Likewise, any location within 500 m of any previous location may indicate the individual is still within a familiar home range or is returning to a previously occupied home range. Although choice of a 14-day acclimation period is subjective, we believe an individual remaining in an area after a 14-day period has gained familiarity with the area. To ensure a valid determination of site familiarity status, we used only those birds for which we had at least three locations prior to 14 days before the time of the predation event.

The movements of two individuals that illustrate basic movement patterns found in the study are shown in Figure 1. Individuals may spend an entire year within a single home range, never moving into unfamiliar space (Figure 1A). Individuals also may exhibit one or more distinct shifts in range throughout a year, with movements through unfamiliar space occurring during these shifts (Figure 1B).

To investigate differences in the effect of movement rate and site familiarity on the risk of being preyed upon by different types of predators, we repeated the above analyses with mortality owing to predation from mammalian and avian predators separately. Finally, to investigate the effect of

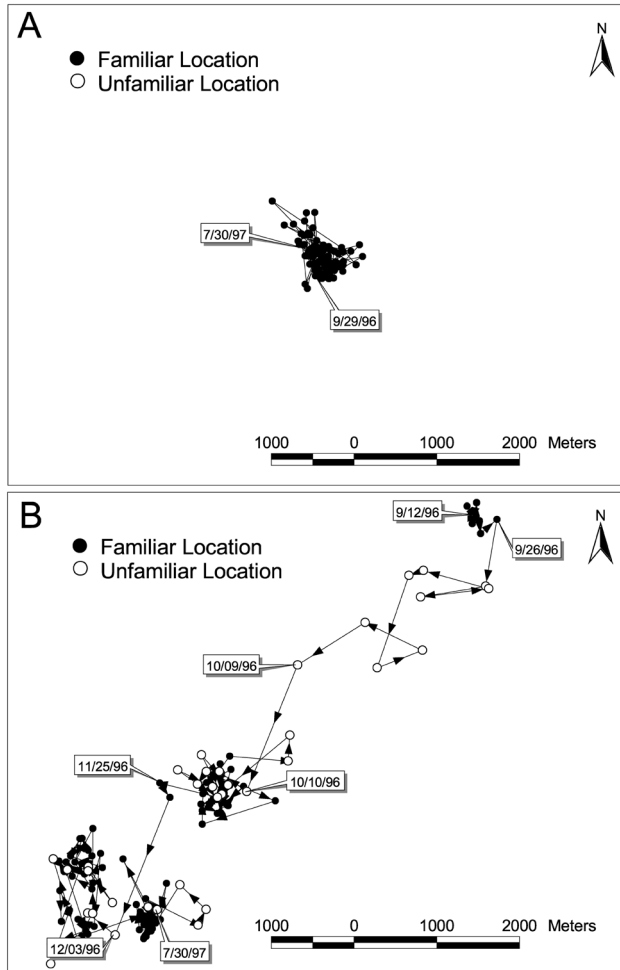


Figure 1
Locations and movement paths for two individual grouse during the study year 1996–1997 that exemplify different movement scenarios. (A) The bird in survived the entire year and exhibited no movement into unfamiliar space. (B) The bird in also survived the year but exhibited at least three distinct shifts into unfamiliar space throughout the year.

movement rate and site familiarity on the risk of being harvested, we repeated the above analyses with mortality owing only to hunting.

RESULTS

During the 3-year study, we obtained usable locations on a total of 193 birds (108 adults and 85 juveniles). The number of usable predation events occurring during this time was 44 for juveniles and 33 for adults. We were able to determine that 24 juvenile and 22 adult mortalities were owing to avian predators, and 13 juvenile and eight adult mortalities were owing to mammalian predators. Because we were unable to calculate a SITE status, we did not include six juveniles and eight adults that were preyed upon. Hunters harvested a total of three juveniles and five adults during the study.

Among juveniles, SITE had a consistently strong effect on the risk of being killed by a predator, with risk being three to 4.5 times greater in unfamiliar than familiar space (Table 1 and Figure 2). The effects of RATE, YEAR, SEX, and STUDY AREA were less obvious, either less consistent between models or having p values between 0.05 and 0.10. Although RATE never had a significant effect (at a significance level of $\alpha =$

Table 1

The risk of predation mortality for juvenile grouse modeled as a function of sex, study area, year, site (familiar or unfamiliar), and three estimates of movement rate

Parameter	Parameter estimate	Wald χ^2	p	Hazard ratio
SEX	-0.51	2.71	.0999	0.60
STUDY AREA	0.66	3.70	.0547	1.93
YEAR	—	0.89	.3432	—
RATE _{capture}	$1.8E^{-4}$	0.03	.8692	1.00
SITE	1.08	7.05	.0079	2.94
SEX	-0.53	2.60	.0964	0.59
STUDY AREA	—	0.78	.3771	—
YEAR	-0.36	3.53	.0601	0.70
RATE _{14day}	-0.003	2.82	.0926	1.00
SITE	1.51	11.97	.0005	4.56
SEX	—	1.80	.1797	—
STUDY AREA	1.43	14.53	.0001	4.16
YEAR	—	0.19	.6597	—
RATE _{3day}	-0.003	2.79	.0946	0.99
SITE	1.27	6.83	.0089	3.57

The Wald chi-square statistic is used to determine if the parameter estimate is significantly different from zero. If the hazard ratio is larger than one, then an increment increase in the variable causes an increase in the risk of predation. Individual variables are defined in the text. There were a total of 85 juveniles tracked, with 44 predation events occurring during the study.

0.05) on the hazard function, RATE_{14day} and RATE_{3day} had $p < .10$ and parameter estimates indicating an increase in mortality risk with decreasing movement rates (Table 1 and Figure 2). One of the models indicated a significant difference in predation risk between sites (Table 1 and Figure 2C). To illustrate model predictions (Figure 2), we used the rate parameter and all parameters with $p < .10$, using the mean predictions for males and females, years, and sites, to calculate the hazard function divided by the baseline hazard (h/h_0). Because the baseline function equals the hazard function when all covariates equal zero (or are left out of the model), h/h_0 is a measure of the overall effect of the covariates on the hazard function.

For adults as for juveniles, SITE had a consistently strong effect on mortality owing to predation, with risk in unfamiliar space being four to 7.5 times greater than in familiar space (Table 2 and Figure 3). Again, SEX, STUDY AREA, YEAR, and RATE were not as strong or consistent in their effects. RATE_{3day} had a significant effect and RATE_{capture} had $p = .07$, both showing increasing mortality risk with increasing movement rate (Table 2 and Figure 3). Two of the models indicated a significant difference in predation risk between years (Table 2 and Figure 3A,B). One of the models indicated a significant difference in predation risk between sites (Table 2 and Figure 3C). Again, to illustrate model predictions (Figure 3), we used the rate parameter and all parameters with $p < .10$, using the mean predictions for males and females, years, and sites.

Because we suspected that movement rate might be correlated with moving through unfamiliar space, we compared the proportion of birds inhabiting familiar and unfamiliar sites in relation to movement rate. We found that although birds inhabiting unfamiliar space tended to move at greater rates than those in familiar space, there was also great overlap in the distributions of movement rates between birds inhabiting the two site types (Figure 4).

Models including predation events owing either only to mammalian or only to avian predators yielded similar results

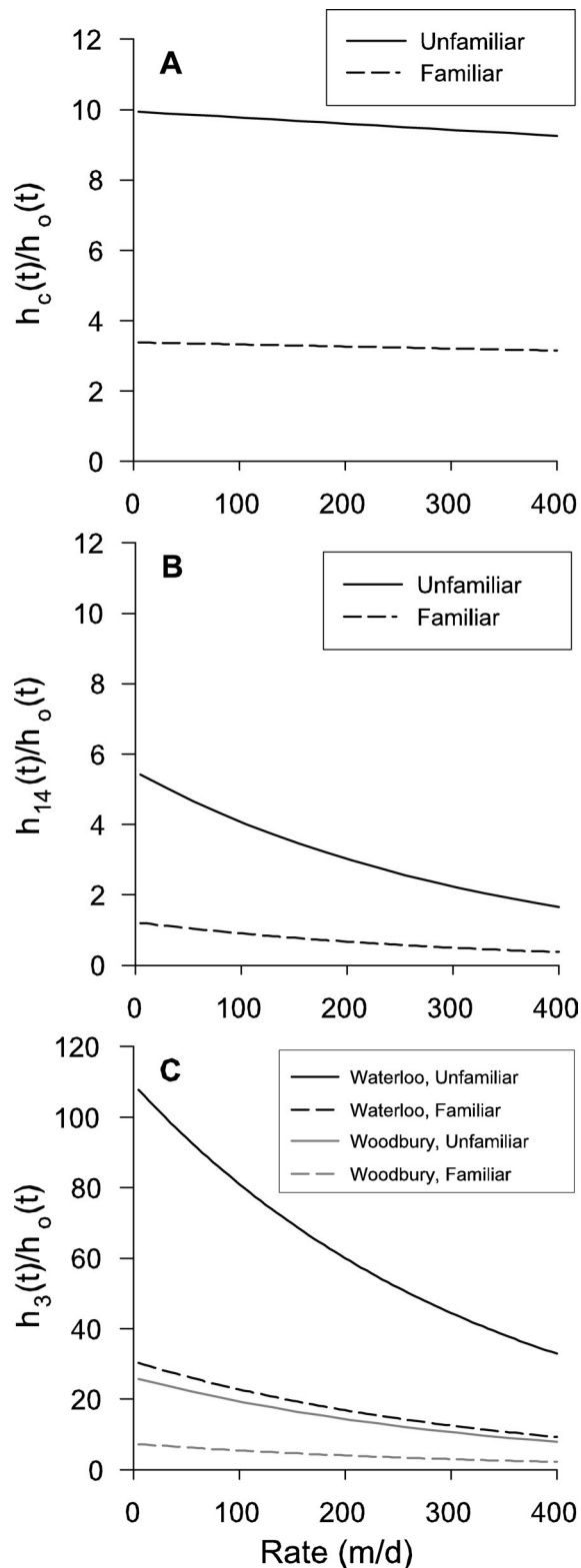


Figure 2
 The juvenile hazard function divided by the baseline hazard (h/h_o) as a function of $RATE_{capture}$ in familiar and unfamiliar space (A), $RATE_{14day}$ in familiar and unfamiliar space (B), and $RATE_{3day}$ in familiar and unfamiliar space (C) in each study area. The effect of SITE was significant in A through C, and the STUDY AREA effect was significant in C. The hazard function divided by the baseline hazard function (h/h_o) is the portion of the overall hazard function ($h[t]$ as specified in Equation 1 in the text) owing to the effects of the model covariates.

Table 2

The risk of predation mortality for adult grouse modeled as a function of sex, study area, year, site (familiar or unfamiliar), and three estimates of movement rate

Parameter	Parameter estimate	Wald χ^2	p	Hazard ratio
SEX	—	0.003	.9602	—
STUDY AREA	—	0.001	.9802	—
YEAR	-0.65	7.40	.0065	0.52
RATE _{capture}	0.005	3.26	.0712	1.01
SITE	1.77	9.68	.0069	4.08
SEX	—	0.04	.8412	—
STUDY AREA	—	0.58	.4465	—
YEAR	-0.77	11.03	.0009	0.46
RATE _{14day}	6.5E ⁻⁵	0.01	.9439	1.00
SITE	2.02	13.77	.0002	7.54
SEX	-0.76	2.72	.0988	0.47
STUDY AREA	1.99	13.65	.0002	7.40
YEAR	-0.44	2.74	.0974	0.64
RATE _{3day}	0.01	4.28	.0385	1.01
SITE	1.54	4.01	.0452	4.68

The Wald chi-square statistic is used to determine if the parameter estimate is significantly different from zero. If the hazard ratio is larger than one, then an increment increase in the variable causes an increase in the risk of predation. Individual variables are defined in the text. There were a total of 108 adults tracked, with 33 predation events occurring during the study.

as those including all predation events. Among juveniles, SITE again had the strongest effect and was significant among all avian predation models and had either significant effects or p values $< .10$ for all mammalian predation models. Among adults, the effect of SITE was significant in all avian and mammalian models, and $RATE_{3day}$ was significant and positive in the model including only avian predation. None of the model covariates had a significant or near significant effect on the mortality risk owing to hunting for either adults or juveniles.

DISCUSSION

Overall, we found inhabiting unfamiliar space to be the only consistently significant factor increasing the risk of being preyed upon for ruffed grouse. The effect of movement rate on predation risk varied greatly in strength between models within an age category and in direction between adults and juveniles. Two of the models for adult birds indicate that increased movement rates may also increase the risk of predation. Although not significant, the effect of increasing movement rates among juveniles was opposite that of adults, with increasing movement rates resulting in a decrease in the risk of predation.

A common assumption in behavioral ecology is that activity increases predation risk owing to movement attracting the attention of predators, thereby increasing the likelihood of predatory encounters (Gotmark and Post, 1996; Lima, 1998). In addition to increasing the risk of predation, movement may have additional consequences during breeding or natal dispersal periods when both distance moved and rate of movement are often greater than during nondispersal periods; dispersing individuals are more likely to suffer costs of high energetic demands (Lima, 1986; McNamara and Houston, 1990; Witter and Cuthill, 1993) and spend time in unfamiliar space (Greenwood and Harvey, 1982) than are nondispersing individuals.

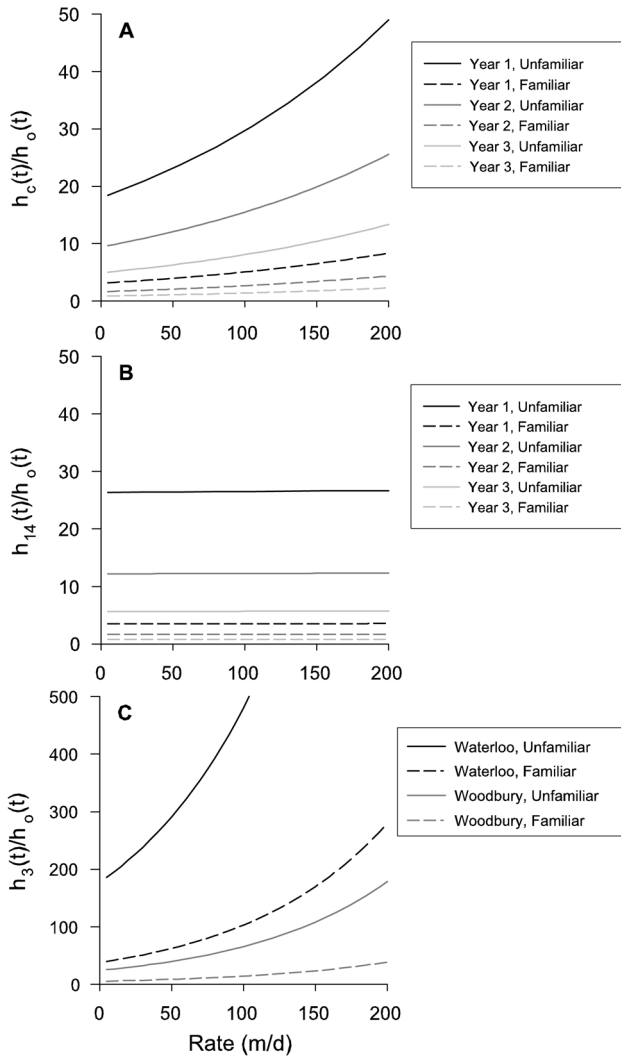


Figure 3

The adult hazard function divided by the baseline hazard (h/h_o) as a function of $\text{RATE}_{\text{capture}}$ in familiar and unfamiliar space in each year (A), $\text{RATE}_{14\text{day}}$ in familiar and unfamiliar space in each year (B), and $\text{RATE}_{3\text{day}}$ in familiar and unfamiliar space (C) in each study area. Significant covariate effects were SITE in A though C, YEAR in A and B, and STUDY AREA and $\text{RATE}_{3\text{day}}$ in C. The hazard function divided by the baseline hazard function (h/h_o) is the portion of the overall hazard function ($h[t]$ as specified in Equation 1 in the text) due to the effects of the model covariates.

Any effect of increased movement rate on predation risk seen in our results may theoretically be a result of movement per se (attraction of predators), inhabiting unfamiliar space, or a combination of both. However, because the model included both the effect of site familiarity and movement rate, our results clearly indicate that unfamiliar space increases the risk of predation independent of any effect of movement rate. In addition, although we found that birds inhabiting unfamiliar space tended to move at greater rates than those in familiar space, the overlap in the distribution of movement rates between the two habitat types (Figure 4) also indicates an independent effect of site familiarity on predation risk. A substantial number of birds moving through unfamiliar space moved at rates comparable to those in familiar space. This provides additional evidence that inhabiting unfamiliar space is dangerous and increases the risk of predation.

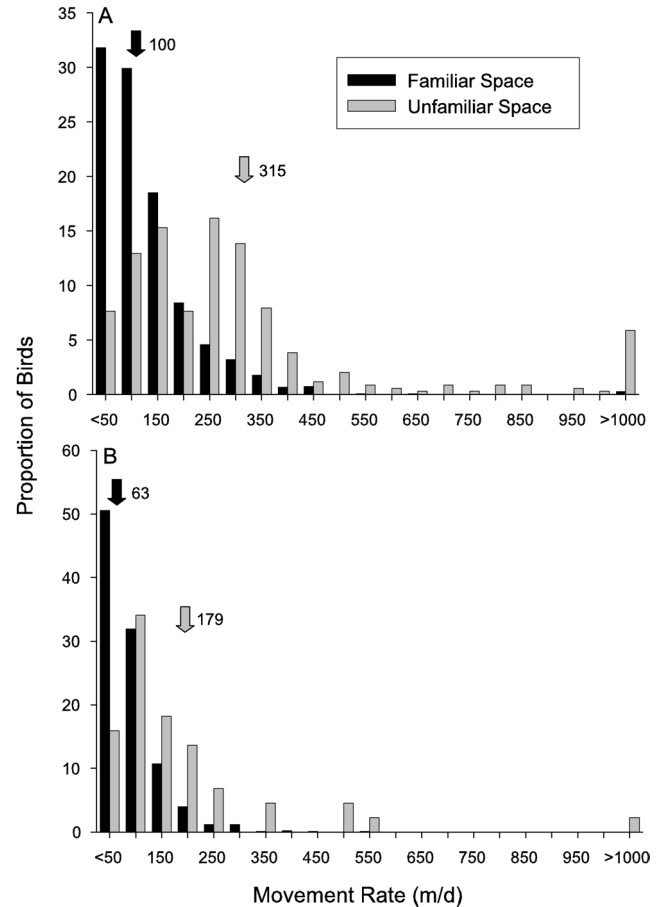


Figure 4

The proportion of juvenile birds (A) and adult birds (B) inhabiting familiar space (dark bars) and unfamiliar space (light bars) in relation to movement rate (m/day) calculated over the time period t to $t - 14$ days). Arrows indicate mean movement rates for birds inhabiting familiar and unfamiliar space.

Individuals moving through unfamiliar space may suffer from decreased foraging efficiency (which also may affect energetic condition) or a decreased ability to avoid predators (Ambrose, 1972; Metzgar, 1967). A defense mechanism used by ruffed grouse is concealment in dense brush and undergrowth. Being in unfamiliar space may compromise this defense mechanism. Grouse moving through unfamiliar space may be more vulnerable to predation during foraging. Lack of experience in a new area may lead to difficulty locating food sources that also provide good cover (e.g., wild grape vines in Ohio). Although we based the analysis on distinguishing between familiar and unfamiliar space, we cannot rule out the possibility that new territory is not only less familiar but also of lower quality (i.e., with less available cover or food sources) than is an individual's original home range.

Although individuals are more likely to inhabit unfamiliar space during the fall dispersal period than at other times of the year, it is unlikely that energy depletion accounts for increased predation risk in this species. Fall is a season of abundant food supply (e.g., mast crops) and a time of significant weight gain for Ohio ruffed grouse (Stoll and McClain, 1988). We believe the cost of unfamiliarity for this species is more likely owing to reduced ability to locate adequate cover or a willingness to inhabit more "dangerous" areas (either with higher predator densities or less available

cover) than from a decrease in energetic condition. High predation risk in unfamiliar space may also account for exploratory behavior exhibited by a substantial proportion of both adults and juveniles in our study. During the fall and spring dispersal periods, these individuals move into unfamiliar space but then return to their pre-dispersal home ranges (Yoder JM, unpublished data).

An increase in predation risk is often assumed to be the cause of differences in survival between dispersers and philopatric individuals (Gaines and McClenaghan, 1980). Unlike most survival studies comparing dispersers and non-dispersers, data from four studies of gallinaceous birds do not indicate a greater mortality risk for dispersing individuals than for philopatric individuals (Beaudette and Keppie, 1992; Hines, 1986; Schieck and Hannon, 1989), including one study examining survival during transience in ruffed grouse (Small et al., 1993). In their telemetry study over a 6-year period in Wisconsin, Small et al. (1993) found no significant differences in survival rates for juvenile ruffed grouse during transient versus colonization (settlement) periods from autumn through spring.

Any effect of increased activity by dispersers would affect predation risk only during the actual transient phase of dispersal. The effects of inhabiting unfamiliar space could affect the predation risk of dispersers both during transience and settlement in a new territory. Small et al. (1993) may have failed to find differences in predation rates between transient and settlement periods because individuals were experiencing effects of unfamiliar space during both phases of dispersal. Because our results indicate the effect of inhabiting unfamiliar space is causing the greatest increase in predation risk, we suspect that most dispersers experience an increase in predation risk during both transience and early settlement periods. Those dispersers with relatively short transient phases and specific foraging or habitat requirements may actually experience the highest predation risk immediately after dispersal has taken place (while settling in a new and unfamiliar territory).

Previous studies attempting to directly measure predation risk in relation to activity cover a wide range of taxa (Daly et al., 1990; Lima, 1998; Norrdahl and Korpimäki, 1998; Skelly, 1994), but not birds. Two studies of small mammals also used radio telemetry to measure movement rates. Daly et al. (1990) found a positive relationship between the rate of movement and predation in a population of kangaroo rats (*Dipodomys merriami*). Norrdahl and Korpimäki (1998) found a similar relationship in field voles (*Microtus agrestis*) and sibling voles (*M. rossiaemeridionalis*). Both of these studies measured only short-term (i.e., hourly or nightly) movement rates. They also did not attempt to distinguish effects of moving through from settling in unfamiliar territory.

Other studies attempting to compare survival rates during the transient portion of dispersal are not only biased toward mammalian species but also rely heavily on mark-recapture techniques (for review, see Béchichon et al., 1996). These techniques tend to underestimate dispersal distances by failing to detect long-range dispersers and are limited in their ability to accurately determine the fate of all individuals (Koenig et al., 1996). The combination of the limited size of most study sites and the inability to distinguish mortality from dispersal beyond trapping range may bias estimates of the survival of dispersing versus philopatric individuals (Daly et al., 1990). The use of radio telemetry can reduce the problem of disappearing individuals by allowing researchers to determine the fate of a much higher proportion of tagged individuals.

Because there exists no expected or control value for what the survival or predation risk would have been for a dispersing

individual had they not dispersed, the true cost of dispersal is impossible to measure (Wolff, 1994). But by comparing a quantifiable measure of activity, and controlling for covariates such as site familiarity between preyed-upon and surviving birds at the time of each predation event, it is possible to provide evidence that dispersers may experience one such cost, an increase in predation risk. The present study highlights another tool to measure possible dispersal costs in addition to traditional comparisons between survival rates of dispersers and philopatric individuals. Our methods should be applicable to most radio-telemetry studies or any study in which individual fates are known and reasonably accurate estimates of movement distances can be made. Direct evidence in other avian species (as well as in other taxa) is sorely needed to support what many ecologists have long suspected; dispersal can be costly.

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