EFFECT OF PREY BIOMASS ON REPRODUCTIVE SUCCESS AND MATING STRATEGY OF BICKNELL'S THRUSH (*CATHARUS BICKNELLI*), A POLYGYNANDROUS SONGBIRD

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ABSTRACT.—Resource availability and distribution are hypothesized to be the primary ecological mechanisms driving variation in avian mating systems. Although food supplementation experiments have been used to examine plasticity in mating strategies, variation in avian mating strategies across naturally occurring gradients of prey availability has rarely been examined. Here, we test the hypothesis that the polygynandrous mating system of Bicknell's Thrush (*Catharus bicknelli*) results from food limitation on female home ranges in the species' harsh montane breeding environment. In 2000, number of chicks fledged per nest was significantly positively correlated with prey biomass on a female's home range, and number of male feeders at a nest was significantly negatively correlated with prey biomass. Neither relationship was significant in 2001, a year with high nest-predation rates, which suggests that nest predation may ultimately limit the species' productivity. These results are consistent with the hypothesis that (1) female productivity is limited by prey biomass, and (2) female mating decisions may be influenced by their assessment of home-range food abundance prior to egg laying. *Received 18 May 2003, accepted 20 December 2003.*

Resumen.—Se hipotetiza que la disponibilidad y la distribución de recursos son los principales mecanismos ecológicos que determinan la variación en los sistemas de apareamiento de las aves. Aunque se han empleado experimentos en los que se suplementa alimento para examinar la plasticidad en los sistemas de apareamiento, la variación en las estrategias de apareamiento de las aves ha sido raramente estudiada a lo largo de gradientes naturales de disponibilidad de presas. En este trabajo ponemos a prueba la hipótesis de que el sistema de apareamiento poliginándrico de *Catharus bicknelli* es consecuencia de la escasez de alimentos en las áreas de hogar que ocupan las hembras en sus hostiles ambientes montanos de reproducción. En el 2000, el número de volantones que emergieron por nido estuvo significativa y positivamente correlacionado con la biomasa de presas en el área de hogar de las hembras, y el número de machos que proveyeron alimentos en los nidos estuvo significativa y negativamente correlacionado con la biomasa de presas. Ninguna de estas relaciones fue significativa en el 2001, un año con altas tasas de depredación de nidos, lo que sugiere que la depredación de nidos podría en última instancia limitar la productividad de la especie. Los resultados son consistentes con la hipótesis de que la productividad de las hembras está limitada por la biomasa de presas, y de que las decisiones de apareamiento de las hembras pueden estar influenciadas por sus evaluaciones de la abundancia y la calidad de alimentos del área de hogar antes de la puesta de huevos.

BOTH EXPERIMENTAL (Boutin 1990 and references therein) and correlative (Newton 1998 and references therein) studies have shown that food availability directly affects avian reproductive success. One mechanism by which this can occur is through changes in mating strategies. For example, in polygamous species, increased food availability can indirectly increase reproductive success through

acquisition of additional mates (Zimmerman 1982, Davies and Lundberg 1984, Wimberger 1988). Indeed, spatial and temporal variation in food resources is one of the key driving forces in the evolution of mating systems (Verner and Willson 1966, Emlen and Oring 1977, Davies 1989, Leisler et al. 2002). However, "optimal" mating strategies may frequently be compromises in which neither sex maximizes its reproductive output (Davies and Houston 1986, Davies 1992). Species with variable mating strategies provide a unique opportunity to

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examine the effects of resource distribution on mating systems. Typically, tests have involved supplemental food experiments. In Dunnocks (*Prunella modularis*), the most extensively studied species in that regard, supplemental food increased polygynandry, decreased polyandry, and increased male mating success (Davies and Lundberg 1985). Natural variation in food availability across home ranges of pairs (or mating associations) can also provide insights as to how individuals make mating and parental-care decisions. However, few studies have measured natural variation in food availability as a means to address how food resources affect mating strategies (but see Eising et al. 2001).

Bicknell's Thrush (*Catharus bicknelli*) is a fir–spruce specialist with a breeding distribution limited to the northeastern United States and southeastern Canada (Rimmer et al. 2001). The species exhibits a polygynandrous mating system in which one female and one to four males feed each brood, and some males simultaneously feed more than one brood (Goetz et al. 2003). Most broods show mixed paternities, and many males sire young in more than one brood (Goetz et al. 2003). Although there are a number of species whose mating systems can best be described as polygynandrous, only the Smith's Longspur (*Calcarius pictus*; Briskie 1992) is known to have a system similar to that of Bicknell's Thrush. One hypothesis for the evolution of this mating system is that a female and single male feeder may be inadequate for provisioning young because of the short breeding season and harsh climatic conditions associated with high-elevation and latitude habitats (*sensu* Briskie 1992, Davies et al. 1995). That hypothesis leads to the prediction that females occupying home ranges with low prey abundance should show decreased reproductive success (i.e. reproductive success should be limited by food supply). Further, if this polygynandrous mating system has evolved to increase male provisioning, then the number of male feeders should be inversely related to food availability on a female's home range. That prediction assumes that females can assess home-range quality and allocate matings accordingly, and that there are negative consequences associated with mating with multiple males (Hartley and Davies 1994). Our study was designed to test these two predictions to provide a preliminary assessment of the ecological factors that drive the unusual mating system of Bicknell's Thrush.

Methods

We conducted our research in Vermont at Mount Mansfield (44°32′N, 72°49′W; hereafter "Mansfield") and Stratton Mountain (43°05′N, 72°55′W; hereafter "Stratton") during the 2000 and 2001 breeding seasons. Vegetation at both sites was dense montane forest dominated by balsam fir (*Abies balsamea*; Rimmer et al. 2001, see Goetz et al. 2003 for additional description of the study sites). Data from radiomarked Bicknell's Thrushes indicated that male home ranges showed substantial spatial overlap, primarily near nest sites (Rimmer et al. 2001). In contrast, female home ranges showed little spatial overlap and therefore were used to delineate prey-sampling areas. We used a 130×130 m (1.69 ha) grid centered on the nest as the prey-sampling area. For intensively monitored female Bicknell's Thrushes ($n = 12$), the mean 95% kernel home range was 2.2 ha (SD = 0.9 ha; Rimmer et al. 2001). Although smaller than the average home range, the 1.69-ha sampling area was greater than the 50% kernel home range of all but one radiomarked female (K. P. McFarland and C. C. Rimmer unpubl. data) and thus corresponds to a core use area.

In each sampling area, 10 sampling points were chosen by randomly selecting an x and y coordinate, each ranging from 0 to 130, with the nest located at the midpoint. Because Bicknell's Thrush forage both on the ground and in the lower canopy, we used sweep-net samples (e.g. Poulin et al. 1993) to sample canopy arthropods and visual counts (Strong 2000) to sample leaf-litter fauna. At each point, we conducted 25 sweeps of the understory (0.1–2 m) foliage with a canvas-bag sweep net, and one visual count, in which we recorded all arthropods observed during a 5-min scan of a 0.25-m^2 quadrat of the leaf-litter surface. For both sampling procedures, all arthropods were categorized by order and size (nearest millimeter). To convert size data to biomass, we developed length–weight regression equations for the major "taxa" encountered in the sweep samples: ants; Coleoptera, Diptera and Hymenoptera combined; Homoptera and Hemiptera combined; holometabolous larvae (primarily Lepidoptera and Hymenoptera); and spiders. For groups for which we did not have adequate sample sizes to develop individual regression equations, we pooled all taxa and developed a composite regression equation. Sample sizes varied from 19 for ants to 51 for holometabolous larvae; r^2 values ranged from 0.75 to 0.98, and all relationships were significant ($P < 0.0001$). Total prey biomass on a female's home range was estimated as the sum of mean biomass for both sampling methods. Although 85% of total biomass was contained in sweep-net samples, there was no correlation ($r = 0.006$, $n = 220$) between biomass in sweep-net samples and visual counts, which suggests that those methods provide different assessments of prey availability.

We located Bicknell's Thrush nests by systematic searches of suitable vegetation and by radiotracking females marked with radiotransmitters attached with leg harnesses (Rappole and Tipton 1991). Bicknell's Thrushes are nearly exclusively single-brooded, although renesting is common after depredation events (Rimmer et al. 2001). Nests were monitored every one to four days. All insect sampling was conducted when nestlings were four to eight days old. To quantify the number of male feeders at a nest, we used video cameras, with a minimum of 6 h of videotape per nest, because 90% of all male feeders could be identified (by unique color leg-band combinations) with 6 h of footage (Goetz et al. 2003).

Prey biomass was similar between Stratton and Mansfield ($t = 1.14$, df = 198.9, $P = 0.25$); therefore data were pooled for analysis. We used linear regression to examine the relationship between prey biomass on a female's home range and (1) number of chicks fledged per nest, and (2) number of male feeders per nest.

RESULTS

During 2000, we found a significant positive relationship between prey biomass on a female's home range and number of chicks fledged from the nest ($r^2 = 0.27$, $F = 6.7$, df = 1 and 14, $P = 0.02$; Fig. 1). We also found a significant inverse relationship between number of male feeders at a given nest and prey biomass on a female's home range ($r^2 = 0.27$, $F = 4.8$, df = 1 and 13, $P < 0.05$; Fig. 2) when one outlier, a nest with no male feeders, was excluded from the analysis. Inclusion of that nest resulted in a nonsignificant relationship ($F = 0.4$, df = 1 and 14, $P = 0.545$). At both sites, nest success was lower in 2001. Mayfield estimates of daily nest-survival rates in 2000 were 0.973 ± 0.013 (SE)

and 0.996 ± 0.004, compared to 0.849 ± 0.007 and 0.935 ± 0.020 in 2001, on Mansfield and Stratton, respectively. In 2001, high nest failure (primarily because of red squirrel [*Tamias hudsonicus*] predation) resulted in only three fledged broods in our two study sites. Thus, sample sizes were too small for proper statistical analysis. However, the trend for the relationship between number of male feeders and prey biomass was similar to that observed in 2000 (Fig. 2). When results from both years were pooled, there was a marginally statistically significant relationship between number of male feeders and prey biomass on a female's home range ($F = 3.3$, df = 1 and 19, $P = 0.08$)

Those results were robust to assumptions regarding the diet of Bicknell's Thrush, because F-statistics were nearly identical whether we included only taxa recorded in the diet of Bicknell's Thrush or taxa that make up at least 10% (numerical abundance) of their diet (based on Rimmer et al. 2001). This was because although prey <4 mm in length made up 78% of the numerical abundance in our samples, they accounted for only 13% of total prey biomass. Consequently, across all samples, a strong correlation exists between total prey biomass (per home range) and biomass of prey >4 mm ($r^2 = 0.997$), which predominate in the diet of Bicknell's Thrush (Rimmer et al. 2001).

DISCUSSION

Our results are consistent with the hypothesis that food abundance during the breeding season on a female's home range is a key ecological
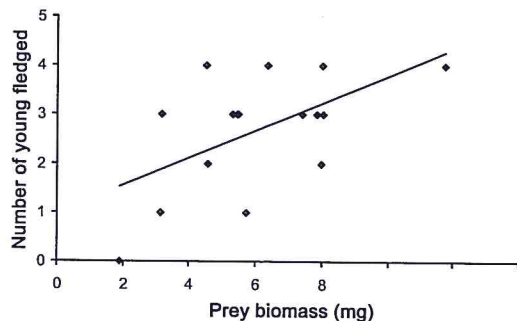

FIG. 1. Relationship between productivity (number of young fledged) in 2000 and prey biomass on a female Bicknell's Thrush home range. Data from Stratton and Mansfield study sites.
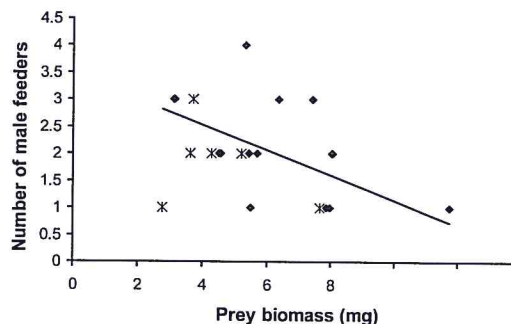
FIG. 2. Relationship between number of male feeders at a nest and prey biomass on a female Bicknell's Thrush home range in 2000 (solid diamonds) and 2001 (asterisks). Regression line is fit to 2000 data. Data from Stratton and Mansfield study sites.

mechanism driving the polygynandrous mating system of Bicknell's Thrush. The negative relationship between prey biomass on a female's home range and number of male feeders at the nest suggests that females may (1) evaluate home-range quality and use that information to gauge both the utility and degree of male provisioning for a given level of available food resources, and (2) allocate copulations to one or more males accordingly. The number of "cooperating" males may ultimately be limited by interference competition among males leading to reproductive dysfunction and egg infertility in females (Hartley and Davies 1994). In a study of the evolution of breeding systems in acrocephaline warblers, Leisler et al. (2002) documented a shift from polygyny in productive habitats to monogamy and additional helpers in poor-quality habitats. Our results provide intraspecific support for that result. Female Bicknell's Thrushes on home ranges with low food availability presumably copulate with multiple males to gain additional provisioning for their broods.

Food manipulation experiments on other species have shown plasticity in mating strategies as a result of environmental variation in food resources. With supplemental food, Redwinged Blackbird (*Agelaius phoenicius*) mating systems shifted from monogamy to polygyny (Ewald and Rohwer 1982, Wimberger 1988), increasing the potential for greater male reproductive success. In Dunnocks, a passerine with a highly plastic mating system, supplemental food decreased female home-range size, thereby increasing the ability of males to monopolize access to females (Davies and Lundberg 1985). Consequently, reproductive success of males increased (greater polygyny) and female reproductive success decreased (less polyandry) in experimental areas. Although we did not measure female home-range size here, matings with more than one male may increase the effective home-range size of females. Because male home ranges overlap multiple females, more male feeders will not only increase the number of provisioning birds but may also give nestlings access to food outside the female's home range.

The positive correlation between prey biomass on a female's home range and number of chicks fledged is similar to results from other studies that have shown higher reproductive success in years with greater food availability or in areas with greater prey availability (see Newton 1998

for a review). For Bicknell's Thrush, however, the relationship is more complex because the number of male feeders at a nest was negatively associated with prey biomass on a female's home range. Additional male feeders might be expected to compensate for the decreased availability of prey, with the result that reproductive success would be constant across nests. Videotape data from nests (Goetz et al. 2003, K. P. McFarland and C. C. Rimmer unpubl. data) suggest that although one additional male feeder increases the proportion of chick-feeding by males, the total proportion of male provisioning exceeds that provided by the female only when three or more males feed a brood. Thus, although females may gain additional assistance in brood provisioning through copulations with multiple males, the contribution of a single male to brood provisioning is substantially less than that of a female (Goetz et al. 2003). As a result, the decision rules for females (regarding allocation of copulations) and males (regarding feeding effort) are likely to lead to conflicts in the "optimal" mating strategy. Removal and food manipulation experiments will be needed to further elucidate these decision rules.

Our results simply address food availability at a single point in time, without considering additional factors that may affect the mating system of Bicknell's Thrush. Because of the frequent bouts of inclement weather at high elevations, temporal variation in prey availability can be extreme and may have influenced the evolution of this species' mating strategy. Additionally, differences in male and female quality may result from genetic (e.g. Møller 1991, Forstmeier et al. 2001), demographic (Ekman et al. 2001), and breeding experience variation in male and female quality (Moreno et al. 2002, Cichon 2003). Thus, assessments of individual quality may play a role in the decision rules of both sexes. The species' skewed sex ratio may also influence annual variation in mating strategy. Although there was no significant difference in sex ratios between years, the slight differences correspond to differences in the average number of male feeders between years.

Intense nest predation during the 2001 breeding season demonstrates that multiple factors likely limit Bicknell's Thrush reproductive success. Rimmer et al. (2001) have reported that balsam-fir cone crops exhibit biennial "boom–bust" cycles, leading to corresponding

cycles in nest-predator populations and reproductive success of the montane bird community. As a result, Bicknell's Thrush productivity may be limited by predation and food availability in alternating years. A similar pattern of reproductive success has been shown in the Rufous-crowned Sparrow (*Aimophila ruficeps*), with the population limited by food and predation depending on stage in the El Niño–Southern Oscillation cycle (Morrison and Bolger 2002). Because of the low population density and patchy breeding distribution of Bicknell's Thrush, only long-term studies will elucidate the relative importance of these factors.

Acknowledgments

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