

MULTIPLE PATERNITY AND MULTIPLE MALE FEEDERS IN BICKNELL'S THRUSH (*CATHARUS BICKNELLI*)

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ABSTRACT.—Although multiple male feeders and multiple paternity for a single brood are taxonomically widespread among nonmigratory birds, they appear to be exceedingly rare among migrants. During a demographic study of Bicknell's Thrush (*Catharus bicknelli*) in Vermont, we observed groups of 2–4 males and one female feed each of 14 broods (78% of 18 broods observed). One male and one female fed each of the remaining four broods. Three males fed broods of two females concurrently or consecutively. Genetic analysis using microsatellite markers revealed multiple paternity in 9 of 13 broods (69%). Four males had offspring in more than one brood in the same year, but no females did. Ten of 17 males (59%) sired offspring in the broods they fed, and 10 of 13 sires (77%) fed the broods in which they sired young. Females fed nestlings more than twice as often as males. Both males and females tended to increase feeding rates as brood size increased. Possible factors influencing the reproductive behavior of Bicknell's Thrush include harsh montane weather, food limitation, a male-biased sex ratio, and reproductive synchrony. Additional research is needed to examine the interaction of ecological and demographic variables that shape the complex breeding ecology of Bicknell's Thrush. Received 25 January 2002, accepted 23 April 2003.

RESUMEN.—Aunque la presencia de varios machos alimentadores y paternidad múltiple en una misma nidada está ampliamente distribuida taxonómicamente entre aves no migratorias, esto parece ser extremadamente raro entre las migratorias. Durante un estudio demográfico de *Catharus bicknelli* en Vermont, Estados Unidos, observamos grupos de 2–4 machos y una hembra alimentando a cada una de 14 nidadas (78% de las 18 nidadas observadas). Un macho y una hembra alimentaron a cada una de las cuatro nidadas restantes. Tres machos alimentaron nidadas de dos hembras al mismo tiempo o consecutivamente. Análisis genéticos usando marcadores microsatélites revelaron la existencia de paternidad múltiple en 9 de 13 nidadas (69%). Cuatro machos tuvieron crías en más de una nidada en el mismo año, cosa que ninguna hembra hizo. Diez de 17 machos (59%) engendraron crías en las nidadas que alimentaron, y 10 de 13 padres (77%) alimentaron las nidadas en las que engendraron crías. Las hembras alimentaron a los pichones con una frecuencia más del doble que la de los machos. Tanto los machos como las hembras tendieron a incrementar sus tasas de alimentación al aumentar el tamaño de la nidada. Los posibles factores que influyen el comportamiento reproductivo de *C. bicknelli* incluyen el clima montano severo, la limitación de alimento, una proporción de sexos sesgada hacia los machos y la sincronía reproductiva. Se necesitan investigaciones adicionales para examinar la interacción entre las variables ecológicas y demográficas que moldean el complejo sistema reproductivo de *C. bicknelli*.

CLASSICAL BEHAVIORAL ECOLOGY theory emphasizes the role of ecology in the evolution of cooperative breeding (Emlen 1982) and other mating systems (Emlen and Oring 1977). Recent empirical findings and theoretical treatments emphasize conflicts of interest among breeding group members and suggest that "breeding systems are the outcome of a battle among compet-

ing interests, with opportunities and constraints set by the environment" (Reynolds 1996). Female reproductive success appears to be limited primarily by resource availability (e.g. prey abundance, critical nutrients, or safe breeding sites), whereas males typically are limited most by access to fertile females (Bateman 1948, Davies 1985). Study of apparently cooperative systems in which multiple reproductively capable adults jointly raise offspring are likely to be particularly revealing of the nature and consequences of the conflicting interests of males and females.

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Polyandrous mating systems with multiple male feeders for single broods are rare but taxonomically widespread among birds, documented in only 13 species representing 10 families (Brown 1987, Hartley and Davies 1994, Ligon 1999). This form of cooperative behavior appears to be especially rare among migratory species and is common in only one migrant North American passerine, Smith's Longspur (*Calcarius pictus*; Briskie et al. 1998). Similar behavior has been well documented in nonmigratory populations of Dunnocks (*Prunella modularis*) in Great Britain (Davies 1992, Davies et al. 1995) and in the altitudinal migrant, Alpine Accentors (*P. collaris*) in Europe and Japan (Hartley et al. 1995; Nakamura 1998a, b).

During research in 1997 on the demography and breeding ecology of Bicknell's Thrush (*Catharus bicknelli*) in montane forests of Vermont, we documented multiple males feeding single-female broods of nestlings. Here, we report preliminary findings on parentage and parental care in Bicknell's Thrush in two disjunct breeding populations in Vermont, and we discuss ecological and demographic factors that may shape the uncommon breeding ecology of this rare, range-restricted species.

METHODS

Study species.—Bicknell's Thrush is a 25–30 g Nearctic–Neotropical migrant passerine that breeds from southern Quebec and the Maritime provinces south through New York and New England, where it is restricted to montane coniferous forest (Ouellet 1993, Atwood et al. 1996, Rimmer et al. 2001). Because of its small global population, estimated at <50,000 individuals (Rimmer et al. 2001), its geographically restricted breeding range, and its dwindling winter habitat, Bicknell's Thrush is considered among the Nearctic–Neotropical migrant species of highest conservation priority in the Northeast (Pashley et al. 2000, Rosenberg and Wells 2000).

Females typically lay three or four eggs per clutch. Incubation and nestling stages both last ~11 days (Rimmer et al. 2001). Females typically produce one brood per year (rarely two) but usually renest after early season failure (Rimmer et al. 2001). The observed population sex ratio on our study plots averaged 1.8 ± 0.4 males (mean \pm SD) for each female (range = 1.5–2.8; Rimmer et al. 2001).

Males are not territorial in the conventional sense (Nice 1941) but instead occupy home ranges that overlap the home ranges of 2–7 other males, encompass 1–4 nests, and average 4.8 ± 2.0 ha (range =

2.2–8.5 ha; 95% fixed-kernel estimates from radio telemetry; Rimmer et al. 2001). In contrast, female home ranges exhibit little overlap and average 2.3 ± 1.0 ha (range = 0.5–4.2 ha; Rimmer et al. 2001).

Field 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"). Vegetation at both sites was dense montane forest dominated by balsam fir (*Abies balsamea*; Rimmer 2001). Nests were found via systematic search (47%), behavioral cues (16%), and by radiotracking females (37%) fitted with tail-mounted transmitters (Wildlife Materials SOPB-2012, Carbondale, Illinois, 0.9 g; or Holohil Systems, BD-2, Carp, Ontario, 1.0 g), using portable receivers (Wildlife Materials TXR-1000) and handheld, three-element Yagi antennae.

Active nests were monitored every 1–4 days; but to minimize the potential effect of our activities on nest success, nestlings were handled only once to band, bleed, weigh, and measure them. Logistical constraints prevented processing all broods at the same age and precluded weight or growth comparisons between broods.

In June–August of 1997–1999 adult thrushes were mist netted and uniquely color-banded to enable identification of individuals. Sex and age (SY = yearling, ASY = after second-year) were determined using standard methods (Pyle 1997), and 50–150 μ L of blood was collected from male ($n = 61$) and female ($n = 25$) adults by brachial venipuncture (Hoysak and Weatherhead 1991). Blood was collected from nestlings ($n = 29$) 4–9 days after hatching, and unhatched eggs ($n = 4$) or remains of dead chicks ($n = 6$) were collected from 15 broods produced by 12 females. We were unable to sample all nestlings for three broods. Blood was stored in plastic vials with 1.0 mL Queen's lysis buffer (Seutin et al. 1991) at 4°C, and eggs and remains were stored at –15°C until DNA extraction.

Feeding of broods was observed directly ($n = 4$) as well as on videotape (Sony CCD-TR516 Hi-8 Handycams; $n = 14$) in 91 video sessions (range = 0.75–4.0 h, total = 293 h). Individual nests were recorded for an average of 14.0 ± 17.9 h (range = 2.6–59.7 h). Adult feeders were identified by color band combinations, breast spot patterns, and female-only behaviors such as brooding.

Laboratory methods.—Parentage was examined using six microsatellite primer sets (Table 1) developed for Swainson's Thrush (*Catharus ustulatus*; Gibbs et al. 1999). DNA was extracted from each whole-blood sample using DNA-ZOL (Chomczynski et al. 1997) and standardized DNA concentrations (Yezerinac et al. 1995). For each microsatellite locus, 50 ng of DNA was amplified from each individual in a 10 μ L polymerase chain reaction (PCR) following Dawson et al. (1997). Polymerase chain reaction conditions were 30 cycles of 94°C for 45 s, X°C for 45 s, and 72°C

for 45 s, where $X^{\circ}\text{C}$, the annealing temperature, was 55°C for $\text{Cu}\mu 05$ and $\text{Cu}\mu 010$, and 53°C for the other four primers. Polymerase chain reaction products were resolved by electrophoresis on 6% denaturing polyacrylamide sequencing gels for 2–4 h at 60V. Gels were dried for 45 min at 80°C and were used to expose Biomax (Dupont) X-ray film in an autoradiograph for 10–200 h, inversely proportional to the dried gel's radioactivity measured with a Geiger–Mueller counter (500–24,000 counts per minute [cpm]). Sizes of PCR fragments were scored using clones of known length as a reference (Dawson et al. 1997). In 60 cases (3.8%, $n = 1,548$ total bands scored) bands were ambiguous, so we assigned no score.

Parentage determination.— Microsatellite alleles are usually autosomal and codominant, are inherited in a Mendelian fashion, and are highly suitable for use in paternity studies (Marshall et al. 1998). We assumed that a mismatch of a single allele ($n = 4$) was due either to a null allele, mutation, or a typing error (Marshall et al. 1998), and we did not exclude parentage in those cases. Parentage was assigned by exclusion, first by determining whether female genotypes matched those of their presumed offspring. Female genotypes matched brood offspring if they possessed either offspring allele at each locus, and males matched if they had the remaining paternal-obligate allele. If the genotypes of two or more males matched an offspring equally well, males were excluded that were not detected within 500 m of nest sites of focal offspring. Extensive daily netting throughout the breeding season to maximize capture probability resulted in few captures of unbanded adults late in the breeding season and gave us confidence that we sampled all, or nearly all, candidate parents on our study sites. Statistical analysis was conducted with STATISTICA for WINDOWS (version 5.5; Statsoft 2000).

RESULTS

Chick feeders.—Of 18 broods monitored during the 1997–1999 breeding seasons (Fig. 1), 1 male feeder was detected for 4 broods (22%), 2 male feeders were detected for 12 broods (67%), 3 males were detected for 1 brood (5.5%), and 4 males were detected for 1 brood (5.5%). Only one female feeder attended each brood. Twelve females contributed a single brood, and three females each contributed two broods (in two different years) to our sample. Twenty-eight males fed those broods. One male fed the brood of the same female in successive years. Two females were each assisted by a pair of males in one year, but by two different males in a subsequent year.

Three males fed broods of two females dur-

TABLE 1. Polymorphism data^a for six microsatellite loci used here.

Locus	k ^b	Hetz ^c	PIC ^d	Excl(1) ^e	Excl(2) ^f
$\text{Cu}\mu 2$	16	0.84	0.822	0.528	0.694
$\text{Cu}\mu 4$	5	0.589	0.506	0.177	0.307
$\text{Cu}\mu 5$	12	0.813	0.786	0.463	0.638
$\text{Cu}\mu 10$	9	0.637	0.58	0.226	0.389
$\text{Cu}\mu 28$	16	0.875	0.856	0.585	0.739
$\text{Cu}\mu 32$	7	0.79	0.752	0.402	0.580

^a Calculated using CERVUS 1.0 (Marshall et al. 1998).

^b Number of alleles.

^c Heterozygosity.

^d Polymorphic information content.

^e Average exclusion probability without information on one parent.

^f Average exclusion probability given information on known parent.

ing the same season, either concurrently ($n = 2$) or sequentially ($n = 1$). The latter male co-fed one brood with a female and another male until the brood fledged. He then began feeding newly hatched nestlings at a second nest, 445 m from the first. As one of two male feeders at the first nest, he fed at about half the rate (1.0 visits per hour) that he fed at the second nest (1.9 visits per hour), where he was the sole male provider.

Chick feeding effort.—Dense vegetation, wind, and variable lighting prevented identification of feeders during 15% of feeding visits. To ensure a high probability of detecting all feeders in our video samples, feeding rates were analyzed only for broods with >6 h observation (by which time 90% of male feeders were detected) and only tapes were used with >80% feeders identified. Average total observation for that subset ($n = 9$ nests) was 21.9 ± 18.2 h (range = 6.0–50.6 h). Four of those broods were fed by a single male, and five were fed by multiple males (Fig. 2). Average share of feeds by females (58%, range = 19–87%; CV = 0.32) was more than twice that of individual males (22%, range = 3–48%, CV = 0.56). Male feeding rates significantly increased with more nestlings in a brood, whereas female rates did not (Table 2). Although combined provisioning rates of both sexes decreased significantly with number of male feeders, neither sex alone fed nestlings at significantly lower rates as numbers of male feeders increased (Table 2). There was no significant relationship between brood size and number of male feeders or proportion of female feeds (Table 2).

Parentage.—Sixty-one adult males, 25 adult females, and 39 offspring were genotyped from 15 broods. All six loci used here were highly polymorphic, showing 5 to 16 alleles and high

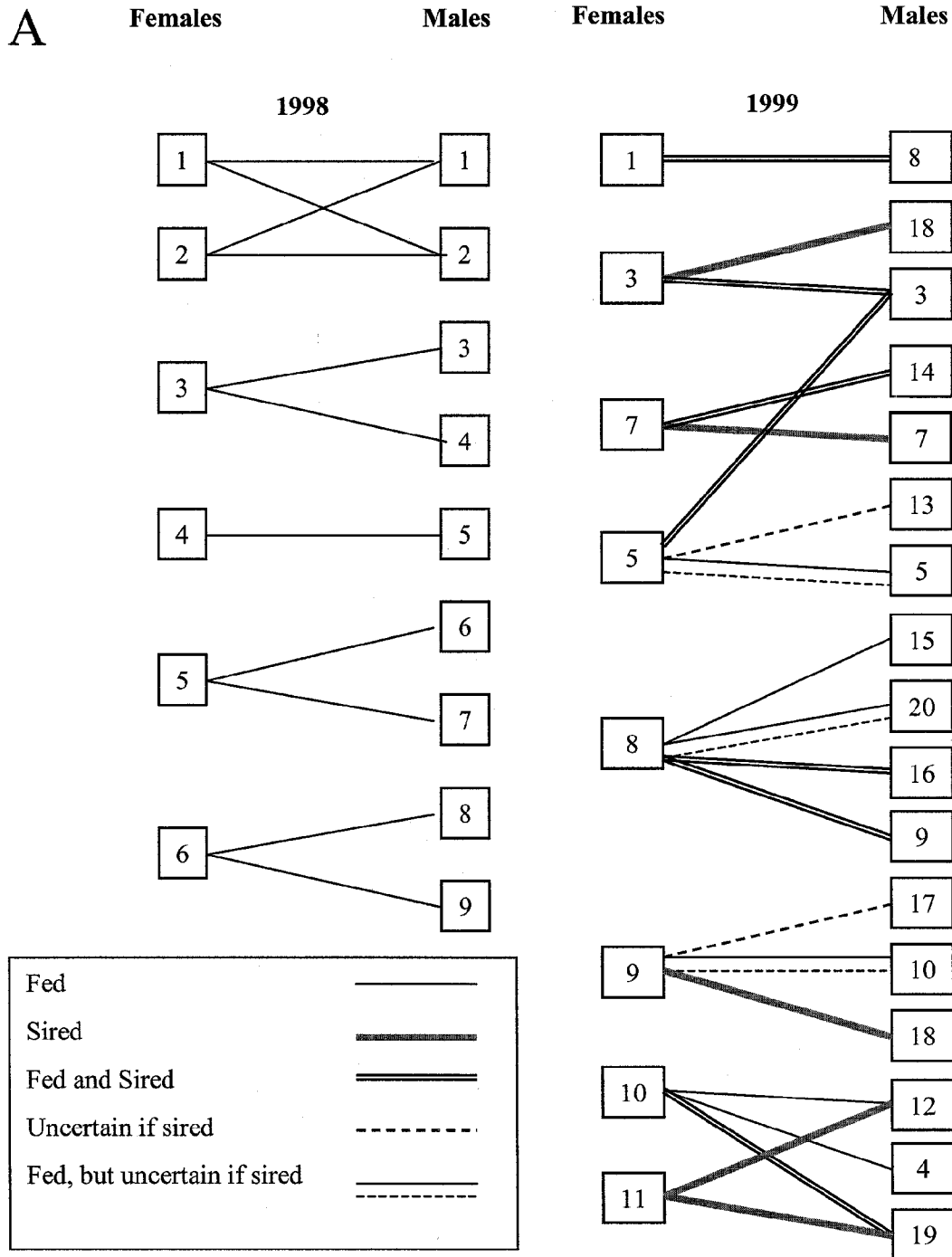


FIG. 1. Feeding and paternity relationships among Bicknell's Thrush on (A) Mt. Mansfield, Vermont in 1998 and 1999. Lines indicate known relationships between males and females. Paternity of Mansfield birds was not determined in 1998; for female 3 in 1999, paternity was determined for only two of three young. There were no feeding data for nestlings of female 11 in 1999. (Continued on next page.)

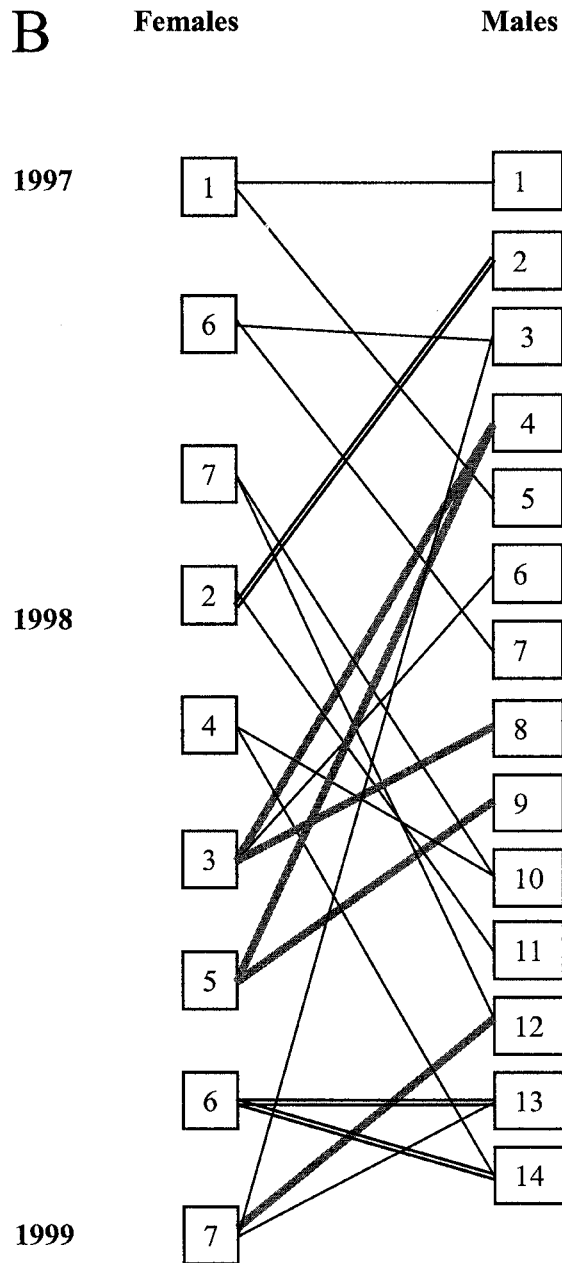


FIG. 1. (Continued.) Feeding and paternity relationships among Bicknell's Thrush on (B) Stratton Mountain, Vermont in 1997–1999. Lines indicate known relationships between males and females. Paternity of all Stratton birds in 1997 and of female 4 in 1998 was undetermined. For female 7 in 1999, paternity was determined for two of three young.

levels of heterozygosity (Table 1). Total exclusion probabilities for the six loci we examined were calculated with CERVUS (Marshall et al. 1998) to be 0.960 for one parent and 0.995 for the second parent.

Of all females genotyped, the brood female was always the best match with all young in her brood. Paternity of 33 of 39 offspring (85%) was determined by genetic exclusion alone, although two of those mismatched the most likely

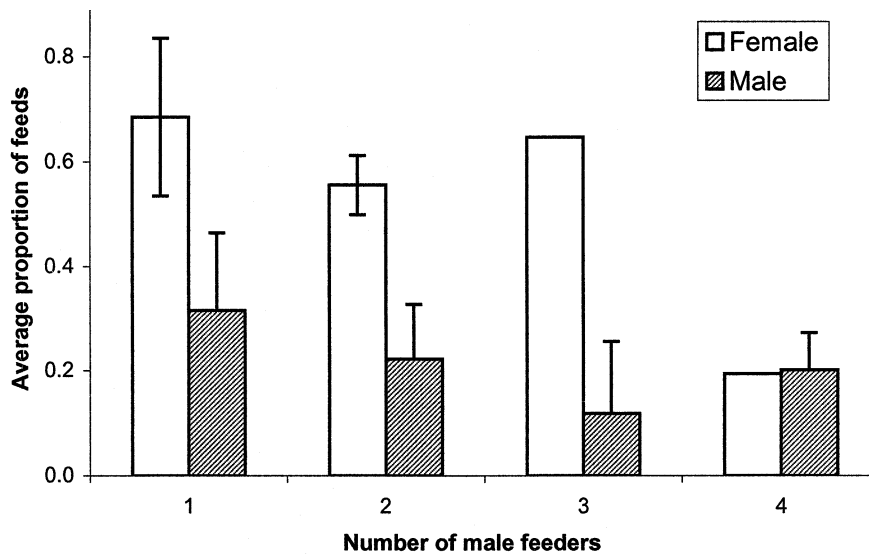


FIG. 2. Average proportion of feeds by females and 1–4 male feeders for nine Bicknell's Thrush broods on Mt. Mansfield, Vermont, 1998–1999. Error bars are ± 1 standard deviation (SD). Broods with one male feeder ($n = 4$), two males ($n = 3$), three males ($n = 1$), and four males ($n = 1$).

father at one locus. Genetic exclusion narrowed paternity of the remaining six offspring to two candidate sires. Of those six, paternity for three offspring was resolved by excluding a candidate whose nearest home range edge was >500 m from the focal nest. Paternity for the remaining three offspring could not be determined in that way because the home ranges of both candidate sires encompassed the focal nest. In one case, both candidates fed the brood.

Of 13 broods, four had a single sire (31%), and nine had two sires (69%). Four males sired

young in broods of two different females in a single year. One male that sired young in two broods fed both broods, whereas another male fed neither. Feeding data are lacking for the other two males. The count of broods with multiple paternity was unchanged by unresolved paternity for three offspring.

Feeding and paternity.—Both feeding and paternity data were obtained for eight broods. Ten males fed the broods in which they sired young, whereas seven males fed broods in which they sired no young (Fig. 1). One male fed one of

TABLE 2. Spearman rank correlations between feeding rates and other variables of broods observed on Mt. Mansfield and Stratton Mt., Vermont, 1997–1999. Bonferroni-adjusted alpha levels for significance is 0.025.

Feeding rates	Variable	<i>n</i>	<i>R</i>	<i>P</i>
Females	Number of male feeders	9	-0.28	0.46
	Number of nestlings	9	0.19	0.62
Males (individually)	Number of male feeders	17	-0.31	0.22
	Number of nestlings	17	0.48	0.05
All feeders (individually)	Number of male feeders	26	-0.41	0.04
	Number of nestlings	26	0.19	0.35
Males (by brood)	Number of male feeders	9	0.48	0.19
	Number of nestlings	9	0.77	0.01
All feeders (by brood)	Number of male feeders	9	0.47	0.20
	Number of nestlings	9	0.58	0.10
Other correlations				
Number of nestlings	Number of male feeders	9	0.07	0.86
	Female feed (%)	9	-0.39	0.30

two broods in which he sired young, whereas another failed to feed either of the two broods in which he sired young.

DISCUSSION

Bicknell's Thrush exhibit a complex, variable breeding system in which females occupy small, non-overlapping home ranges and mate with one or more males who assist in provisioning young. Males, in contrast, occupy large home ranges that overlap extensively with those of both males and females, mate with multiple females, and feed multiple broods concurrently. Similar polyandrous mating systems characterized by multiple males feeding each brood are rare but taxonomically widespread among birds, having been documented in rails (e.g. Jamieson et al. 1994), seabirds (Young 1998), raptors (Faaborg and Patterson 1981, Bednarz and Ligon 1988, Faaborg and Bednarz 1990), and some passerines (e.g. Davies 1992; Davies et al. 1995; Nakamura 1998a, b). A complex breeding system, apparently similar to that of Bicknell's Thrush and termed "female-defense polygynandry", has been described for Smith's Longspur (Briskie 1993). However, the nature of male-male interactions in Bicknell's Thrush is poorly documented, and it is unclear if males in fact physically impede other males from copulating with females. Bicknell's Thrush mating behavior also resembles cooperative polyandry (cf. Faaborg and Patterson 1981, Hartley and Davies 1994), in that breeding associations typically consist of a female and multiple males. The mating system of Bicknell's Thrush differs from classic models of cooperative polyandry (Faaborg and Patterson 1981) and polygynandry (Davies 1985), but is similar to that of Alpine Accentor populations in the French Pyrénées (Hartley et al. 1995) in that males do not appear to defend an individual or group territory. Our small data set of feeding and paternity in Bicknell's Thrush limits inferences but affords some insights into the ecological, demographic, and social factors that may shape this species' unusual breeding ecology.

Male mating strategies.—Parentage data from this study showed that some males and most females (for at least 9 of 13 broods) copulated with multiple partners. Male mating strategies may be relatively straightforward, if males that copulate with multiple partners do so to in-

crease the number of offspring sired (Bateman 1948, Trivers 1972, Davies 1985). Males should prefer monogamy to polyandry (Davies 1992) but may have little choice if mate guarding is ineffective because of dense montane forest vegetation that enables females to elude guarding males. The strong male-biased sex ratio likely intensifies competition among males for copulations, leading to selection for an opportunistic, variable mating strategy.

Female mating strategies.—Females that copulate with multiple partners may do so to acquire genetic benefits including increased brood genetic diversity (Williams 1975) and superior male genes (Hamilton 1990), or direct benefits, such as infanticide deterrence (Davies and Hartley 1996), avoidance of physical punishment from males (Briskie 1993, Smuts and Smuts 1993), and paternal care for offspring (Davies et al. 1996). Although we lack copulation data necessary to examine the relationship between female mating behavior and paternal care, acquisition of paternal care from multiple males may drive female mating behavior in Bicknell's Thrush.

Feeding by multiple males may be important for brood survival if food limitation exceeds the polyandry threshold (Gowaty 1981, Faaborg and Bednarz 1990) so that reproductive success for a male-female pair is lower than for a breeding group with multiple males and a single female. Females mating with multiple males may benefit from increased male provisioning, or by reduced variance in the food supply to offspring (Gowaty 1981, Crook and Crook 1988, Faaborg and Bednarz 1990, Davies 1992). Empirical studies of other species have shown that female reproductive success increases with number of feeding males (Davies et al. 1995, Goldizen et al. 1998, Briskie et al. 1998), that polyandry is most likely on territories with poor food resources (Davies 1992), and that monogamy can replace polyandry when polyandrous females are provided with supplemental food (Davies and Lundberg 1984). For Bicknell's Thrush, arthropod prey biomass on a female's home range is significantly inversely correlated with number of male feeders provisioning her brood but is significantly positively correlated with number of young fledged (A. Strong pers. comm.), which suggests that reproductive output is limited by prey availability.

Provisioning by additional males may even be critical for brood survival during severe montane weather events. Such events, characterized by near-freezing temperatures and heavy rain, are associated with high brood mortality for open cup nesting birds on our study sites (J. E. Goetz et al. unpubl. data). Severe weather likely decreases a female's foraging efficiency while increasing her energetic demands and need to brood nestlings. Experimental manipulations, such as supplemental feeding or male removals, could be used to test whether females benefit from additional paternal care.

The research described here provides a foundation for examining the interaction of ecological and demographic factors that shape the complex breeding ecology of Bicknell's Thrush. Additional research on food limitation, kinship among feeders, and the role of mate quality may yield new insights on intra- and intersexual mating conflicts and cooperation. Study of closely related, allopatric *C. minimus* and *C. fuscescens* and sympatric *C. ustulatus* might elucidate the relative influences of phylogeny (Edwards and Naeem 1993) and environmental factors on the breeding ecology of Bicknell' Thrush.

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