

Male reproductive success and female preference in bushy-tailed woodrats (*Neotoma cinerea*): do females prefer males in good physical condition?

D.M. Weber, J.S. Millar, and B.D. Neff

Abstract: In many mating systems, females may benefit by selecting a male with high genetic quality in the form of good genes or compatible genes. In bushy-tailed woodrats (*Neotoma cinerea* Ord, 1815), previous research has shown that male reproductive success correlates with the mass change of males over the breeding season, indicating that physical body condition may directly influence female choice and hence male reproductive success. We examined male physical condition in relation to reproductive success in the field. Male physical condition was measured as body-mass change over the breeding season, body size, body condition (mass versus size), and anaemia (packed cell volume and mean corpuscular volume). We then conducted trials in the laboratory in which captive females were presented with visual and olfactory cues from two males simultaneously. In the field, males with a low mean corpuscular volume had the highest reproductive success. Captive females also showed a preference for males with low levels of anaemia based on mean corpuscular volume. These results suggest that females are employing a condition-dependent preference.

Résumé : Dans plusieurs systèmes de reproduction, les femelles peuvent tirer un avantage de la sélection d'un mâle de bonne qualité génétique en ce qui a trait à ses gènes supérieurs ou compatibles. Chez les rats sylvestres gris (*Neotoma cinerea* Ord, 1815), des études antérieures ont montré que le succès reproductif des mâles est en corrélation avec leur changement de masse au cours de la période de reproduction, ce qui indique que la condition physique corporelle peut influencer directement le choix des femelles et potentiellement le succès reproductif. Nous examinons la relation entre la condition physique des mâles et leur succès reproductif en nature. Nous avons évalué la condition physique des mâles d'après le changement de masse corporelle durant la saison de reproduction, la taille du corps, la condition corporelle (rapport masse-taille) et l'anémie (hématocrite et volume corpusculaire moyen). Ensuite, à l'aide de femelles en captivité, nous avons fait des essais en laboratoire dans lesquels nous présentons simultanément des signaux visuels et olfactifs de deux mâles. En nature, les mâles ayant un volume corpusculaire moyen faible ont le meilleur succès reproductif. Les femelles en captivité montrent aussi une préférence pour les mâles qui ont un faible niveau d'anémie d'après leur volume corpusculaire moyen. Ces résultats laissent croire que les femelles montrent une préférence qui est basée sur la condition.

[Traduit par la Rédaction]

Introduction

In many mating systems, females are selective in their choice of mate (Andersson 1994; Kokko et al. 2003; Neff and Pitcher 2005). The benefit of this is apparent when females receive direct benefits such as increased parental care or superior resources (Kokko et al. 2003), but it is unclear in systems where there are no direct benefits (males provide only sperm to the female) (Kirkpatrick and Ryan 1991; Andersson 1994). In the latter case, females may benefit by selecting a male with high genetic quality in the form of good genes or compatible genes (Kokko et al. 2003; Neff and Pitcher 2005). For females to assess the genetic quality of males, signalling mechanisms must be employed. In noctur-

nal mammals, odour is recognized as a sexually selected, condition-dependent trait that signals the quality of a male with respect to physical condition and competitive ability (Blaustein 1981; Kavaliers and Colwell 1995; Rich and Hurst 1998; Luque-Larena et al. 2003; Zala et al. 2004).

The bushy-tailed woodrat (*Neotoma cinerea* Ord, 1815) provides an excellent system for studying the link between condition-dependent traits and fitness. In woodrats, males do not provide direct benefits to females (Escherich 1981; Topping 1996). Females may employ mate choice based on the solicitation behaviour of males (Escherich 1981; Fleming et al. 1981) or other indicators of male quality (Topping and Millar 1999). Topping and Millar (1999) found that male reproductive success was related to male mass change over the summer (g/day) and that males with a positive mass change had an increased probability of survival to the next breeding season. However, it is unlikely that females can detect differences in mass change during the time that they breed. Instead, male mass change may relate to other measures of physical body condition that serve as phenotypic correlates of male quality. We examined male mating and reproductive success in relation to measures of male physical body condition in the field and female preference in the laboratory. Physical body condition was assessed using

Received 12 April 2006. Accepted 15 December 2006.
Published on the NRC Research Press Web site at
<http://cjz.nrc.ca> on 27 February 2007.

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measures of mass and morphology as well as indicators of anaemia. We predicted that males in good physical condition would have greater mating and reproductive success in the field than males in poor condition. Similarly, we predicted that females in the laboratory would associate more with males in better physical condition than with those in poor condition.

Materials and methods: field component

Study area and trapping protocol

This study was conducted in the Kananaskis Valley, Alberta, during late April to early September 2004. The main field site was located on four adjacent east-facing outcrops, each 167–370 m long and approximately 1635–1712 m above sea level, with surrounding vegetation typical of montane habitat. All outcrops had been used in previous studies (Hickling 1987; Moses 1992; Topping 1996).

Livetrapping was conducted twice weekly on each outcrop using Tomahawk collapsible traps (model 201, Tomahawk Live Trap Co.) baited with peanut butter and rolled oats, set between 1900 and 2100, and checked between 0630 and 0900 the following morning. Because of the nature of the habitat, traps were placed nonrandomly along outcrops in areas with signs of woodrat activity. The north and east coordinates and elevation of each trapping location were recorded using a global positioning system unit (GPS Pathfinder Pro XL, Trimble Navigation Ltd.).

Trapping locations served as the closest estimate of home ranges and den sites for both males and females. Home ranges were determined using the Home Range Extension (BlueSky Telemetry) for ArcView[®] GIS 3.2a with a 95% minimum convex polygon (MCP) incorporating all of the trapping locations for each woodrat. The use of trapping locations can underestimate home ranges if only part of the home range lies within the trapping area. Therefore, findings based on trapping locations were compared with previous radiotelemetry records for accuracy (Topping 1996). Results from this comparison indicated that our home range sizes were smaller than those found by Topping (1996). However, the patterns of males having larger home ranges than females and the number of males and females with overlapping home ranges were similar. A home range was considered to overlap another if any portion of the home range overlapped, regardless of the degree of overlap. Using the plotted trap locations, we determined the home outcrop for each animal as the outcrop they were trapped on most often, and the den sites of males were approximated as the center of trapping points on the home outcrop. We then calculated the distance from each male's den site to the den site of all other males and females.

Upon capture, each woodrat was transferred to a cloth bag, weighed (± 1 g) using a 1000 g Pesola spring scale, and ear-tagged (Monel No. 1005, National Band and Tag Co.). A tissue sample was taken from each ear (1 mm diameter) for genetic analyses. Tissue samples were placed in 1.5 mL Eppendorf tubes containing 95% ethanol and placed in a cooler before being placed in a 4 °C refrigerator at the field station. Linear measurements were recorded at each capture, including skull length (tip of nose to back of skull, ± 0.1 cm), skull width (greatest width at zygomatic

arches, ± 0.1 mm), and body length (tip of nose to base of tail, ± 0.1 cm), following Topping (1996). Each woodrat was classified as a juvenile (born that year), yearling (1 year old), or older animal (2 or more years old) based on mass or pelage following Topping and Millar (1999). Male reproductive condition was assessed as scrotal (testes descended) or abdominal (testes ascended). Female reproductive condition was recorded as pregnant, lactating, pregnant and lactating, or post-reproductive and perforate or non-perforate. Females with perforate vaginas were considered to be in estrous. Animals were considered to be resident on the study area if they were captured at least once every 2 weeks while females were receptive to males. This period of time was based on the appearance of the first and last weaned offspring of the season by extrapolating the maximum amount of time for gestation and time until weaning for the beginning of the time period (60 days) and the minimum amount of time necessary for the end of the time period (53 days; Hickling 1987).

Overall size was represented by the PC1 scores from a principal component analysis of log-transformed measurements of skull width, skull length, and body length. Body condition was calculated as the standardized residual from a regression of log-transformed mass on PC1 scores. An ordinary least squares (OLS) regression was used following Schulte-Hostedde et al. (2005). Measurements of size and mass were log transformed to ensure homogeneity of variance between the size variables and to standardize variables measured in different units. Average values over the breeding season were used for size and mass calculations. The breeding season was defined per individual based on the length of time the male was recorded as having scrotal testes. Mass change (g/day) was calculated as the slope of a regression of mass on the Julian dates over which a male was recorded as having scrotal testes (Topping 1996).

Collection and analysis of blood samples

Blood was collected in the field from the suborbital sinus of adult males using a 14.61 cm Baxter Pasteur pipette. Males were anaesthetized using Metofane[®] prior to collection of a 0.5 mL sample. Blood was sampled only if males had not been trapped on two consecutive nights because capture two nights in a row could influence blood variables. Blood was collected in an EDTA-coated 1.3 mL microtube and placed in a cooler with ice. At the field station, anaemia (Bell 2002) was measured as packed cell volume (PCV) and mean corpuscular volume (MCV). PCV was measured twice for each sample by drawing blood into two 75 μ L microhematocrit tubes (Fisher Scientific) and centrifuging the samples at 13 000 g in an IEC MB microhematocrit centrifuge for 7 min. Then 0.3 mL of each baseline blood sample was subsampled and sent to Calgary Laboratory Services (Calgary, Alberta) for determination of PCV and MCV.

Microsatellite DNA analysis

In the laboratory, ear tissue samples were soaked in distilled water for 1–4 h to remove any trace of ethanol remaining from the preservation process. The DNA from each tissue was then isolated using the Sigma-Aldrich GenElute[™] Mammalian Genomic DNA Miniprep kit. The extracted

DNA was stored in a freezer at -20°C until polymerase chain reaction (PCR) was conducted.

PCR was conducted using a 10 μL mixture comprising 2 μL of DNA template, 3.5 mmol/L MgCl_2 (Sigma-Aldrich), 1 \times PCR Buffer (Sigma-Aldrich), 0.2 mmol/L deoxynucleotide mix (Invitrogen), 0.02 units/ μL Taq DNA polymerase (Sigma-Aldrich), and 0.5 mmol/L of the forward and reverse primers (Prologo). DNA was amplified using primers for up to five loci (primers in Castleberry et al. 2000). The forward primer was fluorescently labelled (Nma01, Nma04, Nma10, and Nma11 by D4-PA blue and Nma08 by D2-PA black; Beckman Coulter). Amplification of loci Nma01, Nma04, Nma10, and Nma11 was conducted using a Whatman Biometra TGradient thermocycler with the following program: (1) 120 s at 94°C ; (2) 30 s at 94°C ; (3) 30 s at 54°C ; (4) 60 s at 72°C ; (5) repeat steps 2 to 4 for 34 cycles; (6) 420 s at 72°C . Amplification of Nma08 was conducted using a Whatman Biometra T1 thermocycler with the following program: (1) 120 s at 94°C ; (2) 30 s at 94°C ; (3) 30 s at 50°C ; (4) 60 s at 72°C ; (5) repeat steps 2 to 4 for 29 cycles with a 0.15°C decrease in annealing temperature (step 3) each cycle; (6) 420 s at 72°C . Alleles were determined using a CEQTM 8000 Genetic Analysis System (Beckman Coulter) and associated fragment analysis software. Alleles for Nma01, Nma08, Nma10, and Nma11 were determined for all individuals, but alleles for Nma04 were determined only if necessary (see below).

Litter size and maternity and paternity assignment

We assigned parent-pairs for each offspring using a C++ program. To ensure that no candidate parents were excluded because of mutation or typing error, possible parents were excluded only if they differed by more than 4.0 bp (2 repeat units). If there were more than one matching parent-pair ($n = 21$), livetrapping data were used to confirm the parent-pair ($n = 21$). If there was ambiguity regarding the true parent-pair, an additional locus (Nma04) was amplified ($n = 9$).

Traits associated with reproductive success

Mating success in the field was defined as the number of litters that a male sired from which one or more offspring were weaned. Reproductive success was defined as the number of weaned offspring that a male sired. Owing to the strong correlation between reproductive success and the number of litters produced (Spearman's rank correlation; $r = 0.949$, $n = 11$, $p < 0.001$), only reproductive success was examined in relation to male physical condition. In the laboratory, female choice, as measured by the proportion of time a female spent with a male in preference trials, was examined in relation to male physical condition. Male physical condition variables included mass change, body condition, size, PCV, and MCV.

Apart from female choice, components of male-male competition can also affect the reproductive success of males, including the ability of a male to gain access to multiple females (Andersson 1994). Therefore, the number of males and females with overlapping home ranges and the average distance to the den site of the two nearest males or females were included in analyses of reproductive success in the field.

Spearman's rank correlations were used to investigate

whether or not trapping or the number of trials males were used in had an effect on physical condition. The number of times trapped or used in trials corresponded to the date of blood sampling for blood variables and length of the breeding season for all other variables. Bonferroni sequential correction was used for Spearman's rank correlations using the number of times trapped (5 tests) and the number of trials used in (3 tests) because each involved using the same data set for multiple tests.

We used a stepwise multiple linear regression to determine the effect of physical condition and male-male competition traits on reproductive success. Criteria for entry or removal of variables were $F \geq 3.84$ and $F < 2.71$, respectively. Owing to a lack of normality, PCV was transformed as the negative inverse of the square root.

Materials and methods: laboratory component

Preference trials

Preference trials were conducted using males from the study site. Resident scrotal males were moved from the main study area to the laboratory in the morning, placed in plastic cages, and given fresh vegetation and water ad libitum. The pair of males used for each trial depended on which males were caught in the field that day. Trials were conducted between 1200 and 1830 and the males were returned to the field the same day.

Adult females used in trials were captured between mid-March and early June 2004 on outcrops located at least 3 km from the main study area to eliminate familiarity with males. Females were held in captivity for the duration of trials and were housed at room temperature in a photoperiod consistent with the natural photoperiod. They were housed individually in plastic (0.59 m \times 0.31 m \times 0.23 m) or metal (1.0 m \times 0.5 m \times 0.4 m) cages containing wood chips, bedding, and a large can for shelter and given water and rat chow (LabDiet[®] 5001, PMI Nutrition International), sunflower seeds, oats, and fresh vegetation (mainly dandelions (*Taraxacum officinale*), buffaloberry (*Shepherdia canadensis*), trembling aspen (*Populus tremuloides*), and willow (*Salix* spp.)) ad libitum. Female reproductive status was monitored weekly and only females in estrous were used in trials.

For each preference trial, a female was placed in a 35 cm \times 15 cm \times 15 cm Plexiglas[®] chamber connected to the neutral arm of a Y-shaped Plexiglas maze with arms of equivalent length (95 cm \times 15 cm \times 15 cm). A red light illuminated the room. The female acclimatized for 5 min. Then, two males, individually placed in 35 cm \times 15 cm \times 15 cm Plexiglas chambers lined with filter paper to absorb glandular deposits, urine, and faeces, were connected simultaneously and randomly to the arms of the maze. Following a procedure similar to that of Drickamer et al. (2000), a 17 cm \times 17 cm mesh screen was placed between the male chambers and the maze arms to allow females and males to obtain olfactory and visual cues, but not copulate. The female was then given access to the entire maze for 300 s and a video camera (Sony Handycam TRV118) was used to record female activity. Videotapes were then viewed to record how much time the female spent with each male, as

defined by the amount of time she was in each arm of the maze. Female preference was measured as the number of seconds a female spent with a given male divided by the total number of seconds spent with both males. Between trials, the maze was disassembled, cleaned using 10% bleach and water, thoroughly dried, and reassembled.

Traits associated with female choice in the laboratory

Female preference was examined in relation to male physical condition. Male physical condition variables included mass change, body condition, size, PCV, and MCV, all measured in the field.

A one-sample *t* test was used to determine whether female preference for a male differed from 0.5 (equal preference for both males). If a female was used in more than one trial, her preference scores were averaged. Only trials in which females exhibited a minimal level of responsiveness (showing interest for 10 or more seconds per male) were included. Most males were used in more than one trial. However, trials were included in the analysis only if the male had been presented to a female only once. Bonferroni sequential correction was used because the times attained for the preference trials were used in multiple tests.

Data were analysed using SPSS 13.0 (SPSS Inc., Chicago, Illinois, USA) with a statistical significance level of $p < 0.05$. Assumptions for parametric tests were met in all cases.

Results

Eleven and 13 resident breeding males and females, respectively, were captured on the study site between 26 April 2004 and 1 September 2004 (mean number of times captured = 23.2 (SD = 8.0)). Only 9 of the 13 females were used in the preference trials because fluctuations in the estrous cycles of the other 4 did not coincide with the timing of the trials. One additional breeding, but not resident, male was captured on the study site for part of the breeding season and was used in one preference trial. One resident male was not used in any of the preference trials. For this reason, tests used to investigate confounding effects on both the field and the laboratory component had a sample size of 12, whereas tests examining only the field or the laboratory component had a sample size of 11. After Bonferroni correction, there was no significant relationship between the number of trials or the number of times trapped and mass change, PCV, or MCV. However, there was a positive trend between body condition and size and the number of laboratory trials (Spearman's rank correlation: $r_s = 0.436$, $n = 12$, $p = 0.16$ and $r_s = 0.671$, $n = 12$, $p = 0.017$, respectively; Bonferroni-adjusted significance level was 0.017 and 0.010, respectively) and the number of times trapped in the field (Spearman's rank correlation: $r_s = 0.623$, $n = 12$, $p = 0.031$ and $r_s = 0.587$, $n = 12$, $p = 0.045$, respectively; Bonferroni-adjusted significance level was 0.017 and 0.025, respectively), indicating that males of larger size or greater body condition might be more active and captured more often than males of small size or poor body condition. Therefore, an additional correlation was run between the number of times trapped and reproductive success.

Separate principal component analyses were conducted for size in the field and size in the laboratory because each

included different males. For males in the field ($n = 11$) and those in the laboratory ($n = 11$), PC1 explained 74% and 61% of the variation in the analysis, respectively. Measures of skull width, skull length, and body length loaded positively for PC1 (field: 0.95, 0.79, and 0.83, respectively; laboratory: 0.85, 0.73, and 0.75, respectively).

Male–male competition

The average number of males overlapping a male's home range was 5.6 (SD 1.8, range 3–9). The average number of females overlapping a male's home range was 7.3 (SD 2.8, range 4–13). Male home range averaged 1.46 ha (SD 1.53, range 0.12–4.29). The average distance to the den sites of the two nearest females ranged from 20.9 to 128.3 m and averaged 71.2 m (SD 41.2). The average distance to the two nearest males ranged from 18.1 to 110.1 m and averaged 61.9 m (SD 29.7).

Litter size, maternity, and paternity

A total of 34 juveniles were captured on the study site. Of these, 7 were not born on the outcrop on which they were captured based on mass at first capture in relation to female breeding chronologies and 4 were not born on the outcrop according to genetic analyses. Eleven litters, with a total of 23 juveniles, were assigned to parents on the study site. Three females weaned two litters each. In two cases, the females mated with the same male twice. Only males residing on the study site fathered offspring born on the study site, although 7 of 11 litters were sired by males that were not resident on the female's outcrop. Ten of 11 litters were sired by a male with a home range overlapping the female's home range. There was no age-related difference in reproductive success among males. However, there was a tendency for old males to have higher reproductive success than young males (older male vs. yearling, Mann–Whitney *U*: $n = 11$, $p = 0.11$).

Physical condition, male–male competition, and reproductive success

A stepwise multiple linear regression analysis yielded a single-factor equation relating reproductive success to MCV ($R = 0.666$, $df = 2$, $p = 0.025$; Fig. 1):

$$\text{Reproductive success} = -1.006\text{MCV} + 46.195$$

No other factors were significant.

A correlation between the number of times a male was trapped during the breeding season and reproductive success indicated there was a strong positive relationship between these variables (Pearson correlation; $r = 0.685$, $n = 11$, $p = 0.020$; Fig. 2).

Physical condition and female preference

Eleven breeding males and 9 estrous females were used in the preference trials. There was no effect of side of the Y maze or Julian date on the time a female spent with a male (Mann–Whitney *U*: $n = 30$, $p = 0.28$; Spearman's rank correlation: $r_s = -0.005$, $n = 15$, $p = 0.99$, respectively). There was also no effect of time of day on the time a female spent with both males (Spearman's rank correlation: $r_s = -0.164$, $n = 15$, $p = 0.56$).

Fig. 1. Number of offspring sired by a male bushy-tailed woodrat (*Neotoma cinerea*) in relation to his mean corpuscular volume (fL). A stepwise multiple linear regression indicated a statistically significant relationship ($R = 0.666$, $df = 2$, $p = 0.025$) with a linear fit described by the function $y = -1.006x + 46.195$.

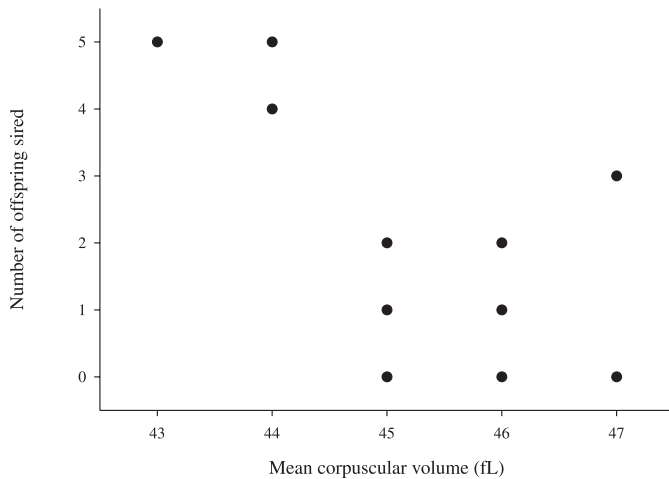
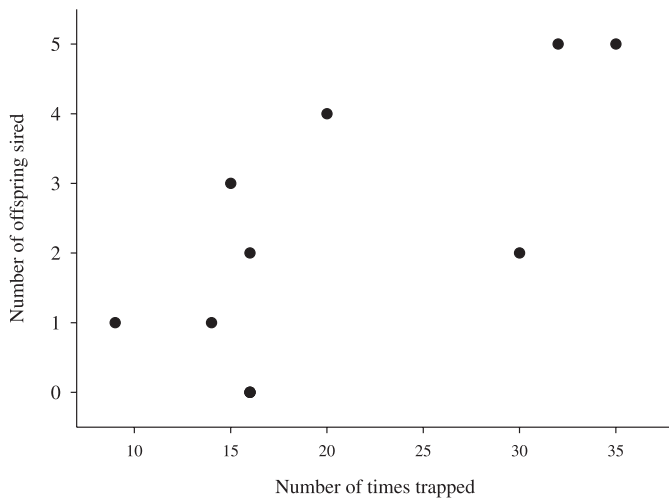


Fig. 2. Number of offspring sired by a male bushy-tailed woodrat in relation to the number of times he was trapped during the breeding season. A Pearson correlation analysis indicated that the correlation was statistically significant ($r = 0.685$, $n = 11$, $p = 0.020$).



The total number of trials (previous trials plus current trial being conducted) had no effect on the time spent with a male in the current trial (Spearman's rank correlation: $r_s = -0.086$, $n = 30$, $p = 0.65$). In cases where the same pair of males was used with multiple females on the same day, there was no effect of the number of trials a male was used in that day (1, 2, or 3 trials) on the time spent with a male (Kruskal–Wallis H : $n = 30$, $p = 0.26$). There was no effect of male age (older male or yearling) on the time spent with the male (Kruskal–Wallis H : $n = 30$, $p = 1.00$). There was a significant correlation between male responsiveness to females (proportion of times a male was active in response to a visit by the female) and the relative preference for that male (Spearman's rank correlation: $r_s = 0.409$, $n = 30$, $p = 0.009$). However, there was no effect of the number of preference trials that a male was used in on male activity

(overall number of trials: Spearman's rank correlation, $r_s = 0.038$, $n = 30$, $p = 0.84$; in one day: Kruskal–Wallis H , $n = 30$, $p = 0.68$).

The number of trials a female was used in (1, 2, or 3 trials) had no effect on the time she spent with both males (Kruskal–Wallis H : $n = 15$, $p = 0.93$). There was a tendency for female responsiveness (met minimum responsiveness, yes or no) to differ between females with and without breeding experience (χ^2 : $df = 1$, $p = 0.08$).

Female preference times (i.e., time spent with a male) ranged from 11 to 269 s (mean = 82.80, SD = 66.04) out of a possible 300 s. Twenty-three trials were conducted. One-sample t tests indicated that after Bonferroni correction relative female preference differed significantly from 0.5 for males with low MCV ($t = -4.488$, $df = 8$, $p = 0.002$; Fig. 3; $\alpha = 0.010$ with Bonferroni correction) but not in relation to mass change ($t = 0.932$, $df = 8$, $p = 0.09$), size ($t = 0.135$, $df = 8$, $p = 0.31$), body condition ($t = 1.081$, $df = 8$, $p = 0.90$), or PCV ($t = -1.909$, $df = 8$, $p = 0.09$). However, there was a tendency for relative female preference to differ from 0.5 for males with higher mass change (Fig. 4) and lower PCV (Fig. 5).

Discussion

Based on both field and laboratory studies, condition-dependent mate choice or preference occurs in this population of bushy-tailed woodrats. More specifically, males with lower MCV had greater reproductive success and were also preferred by females over males of higher MCV. While many studies have linked condition-dependent traits to female preference in the laboratory or reproductive success in the field (Topping and Millar 1999; Wagner and Hoback 1999; Luque-Larena et al. 2003; Rantala et al. 2003; Schulte-Hostedde and Millar 2004; Zala et al. 2004), no study, to our knowledge, has used the same males to assess mating patterns and preference both in the laboratory and in the field.

Results from the field study indicated that there was a significant negative relationship between MCV and reproductive success. Such a relationship was consistent with our expectations because a higher MCV is indicative of anaemia (Dein 1986), implying that females actively prefer males with lower levels of anaemia. Numerous studies have addressed the positive relationship between added stress on an organism and MCV (black bears: Hellgren et al. 1993; great skuas: Kalmbach et al. 2004). Because stress is often reflected in the overall condition of animals (Buchanan 2000), MCV should give some indication of a male's overall condition. However, few studies have addressed the potential for MCV values to influence reproductive success in a non-resource based system. Bearhop et al. (1999) found that male great skuas (*Stercorarius skua* (Brünnich, 1764)) in good condition, based on MCV, fledged more chicks than those in poor condition. Their study involved a mating system in which parental care plays a role in offspring success, whereas ours does not. Discrimination of mates using MCV suggests that odour might be important in female choice because previous studies using hematocrit levels (or PCV) found that females preferred the odour of less anaemic males (Luque-Larena et al. 2003). In addition,

Fig. 3. Proportion of time a female spent with the male with the higher mean corpuscular volume (MCV) and the difference in the MCV of the two males presented to the female in a preference trial (higher – lower male) ($t = -4.488$, $df = 8$, $p < 0.002$). Proportion of time was measured as the time spent with the male of higher MCV divided by the time spent with both males. The preference time for an MCV difference of zero can be interpreted as being higher or lower depending on which male is listed as the higher MCV male, so this point was not included in the statistical analysis. A dashed line represents equal proportions of time spent with both males. Symbols and corresponding numbers represent different females.

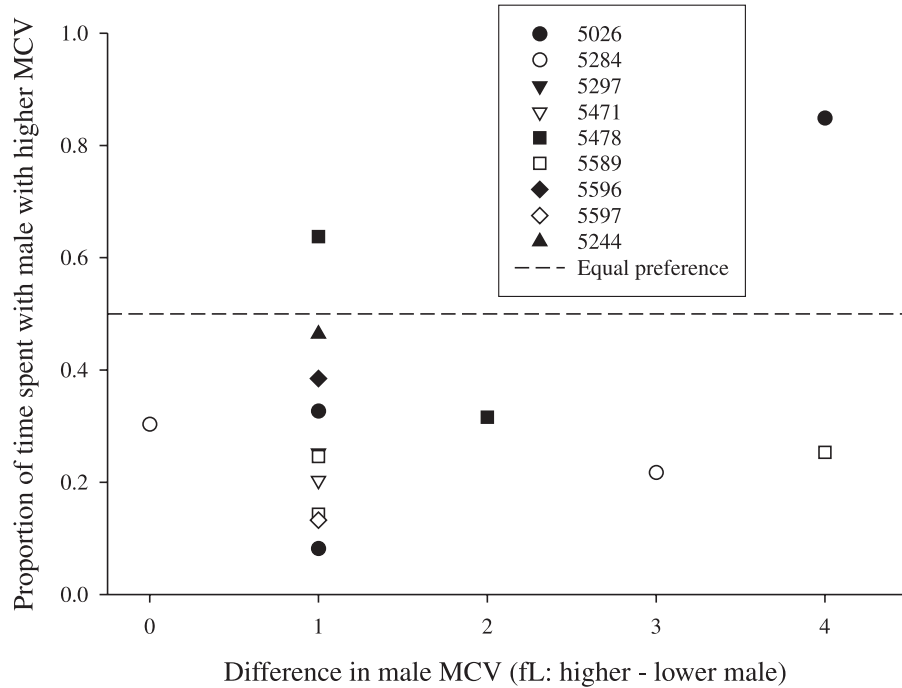


Fig. 4. Proportion of time a female spent with the male with the greater mass change (g/day) and the difference in the mass change of the two males presented to the female in a preference trial (higher – lower male) ($t = 0.932$, $df = 8$, $p < 0.093$). Proportion of time was measured as the time spent with the male of greater mass change divided by the time spent with both males. The dashed line represents equal proportions of time spent with both males. Mass change (g/day) was the slope of a regression of mass on the length of the breeding season (males scrotal or with testes descended). Symbols and corresponding numbers represent different females.

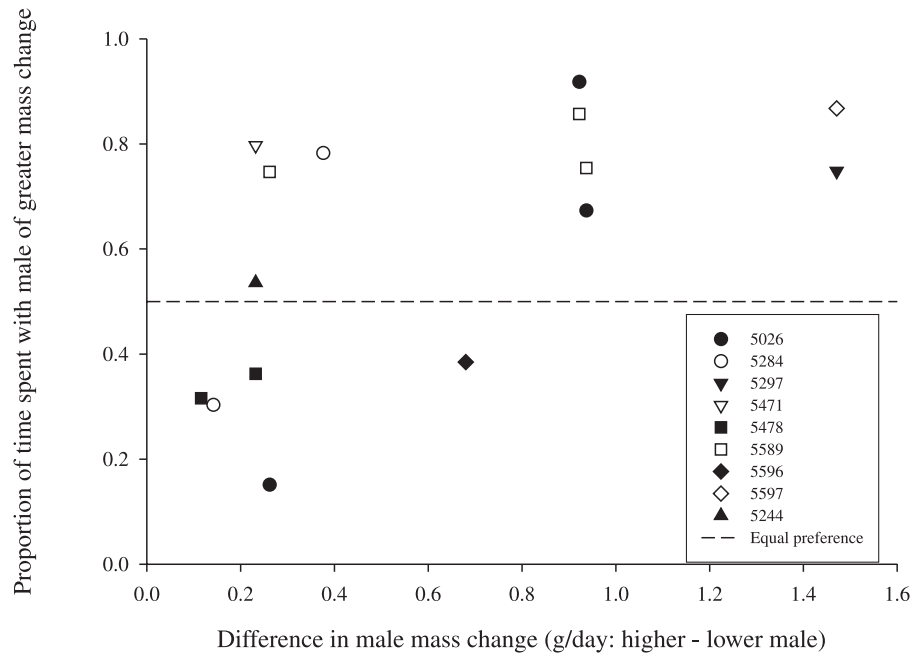
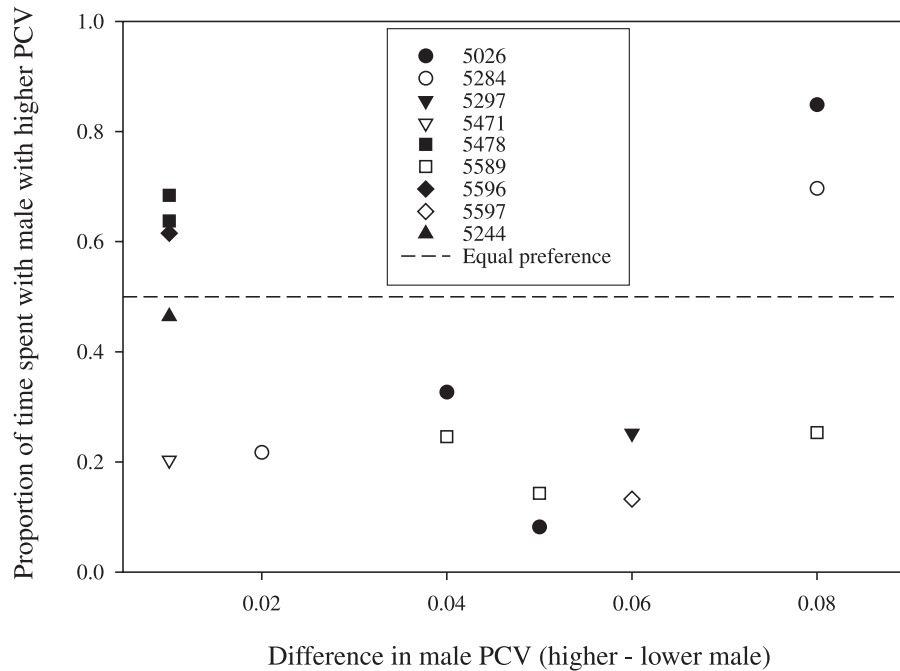


Fig. 5. Proportion of time a female spent with the male with the higher packed cell volume (PCV) and the difference in the PCV of the two males presented to the female in a preference trial (higher – lower male) ($t = -1.909$, $df = 8$, $p < 0.093$). Proportion of time was measured as the time spent with the male of higher PCV divided by the time spent with both males. The dashed line represents equal proportions of time spent with both males. Symbols and corresponding numbers represent different females.



there was a strong relationship between the number of times a woodrat was trapped and reproductive success, suggesting that males trapped more frequently were more active in general and may also have been more active in pursuing females. Unlike Topping and Millar (1999), we found no strong evidence that males with greater changes in mass had higher reproductive success. This may have been due to our small sample size or low variation in mass change, with most males having a positive mass change over the season. Furthermore, the lack of any significant partial correlation for factors of male–male competition suggests that intrasexual competition does not dictate mating patterns in woodrats.

Results from the preference trials indicated that females preferred males with lower MCV and that there was a tendency for females to prefer males with greater mass change and lower PCV. The findings regarding MCV were consistent with the results obtained in the field, and the tendency for females to prefer males who gained more mass over the breeding season was consistent with previous studies of bushy-tailed woodrats and field crickets (Topping and Millar 1999; Wagner and Hoback 1999).

Because we did not allow females to copulate with males during the preference trials, we cannot confirm that a preference for males in trials would actually lead to mate choice. However, previous studies suggest that a preference displayed toward a male without copulation may be followed through on when the animals are given a chance to mate. Drickamer et al. (2000) conducted preference trials in which females could see, smell, hear, and make tactile contact with males through wire mesh. They then allowed some females to mate with their preferred male, while others were given only the option to mate with the nonpreferred male. Females

allowed to mate with preferred males produced significantly more litters than those that mated with nonpreferred males. In addition, the offspring produced from preferred matings were more successful in dominance contests and nest building and had a higher tendency to survive until 60 days, indicating that free female mate choice has implications for reproductive success.

Although our laboratory trials indicated a trend between mass change and female preference, mass change was not a strong factor influencing reproductive success in the wild. This apparent discrepancy could arise if captive females can be more choosy when selecting a male than females sequentially encountering potential mates in the wild. In the field, the increased cost of searching for a male or assessing male quality may decrease the choosiness of a female (Fawcett and Johnstone 2003). The tendency for females to prefer males with lower PCV is difficult to explain, as we expected females to prefer males with higher PCV because nutritional stress can result in a decline in hematocrit levels (Morton 1994). However, Dawson and Bortolotti (1997) found that hematocrit levels in the American kestrel (*Falco sparverius* L., 1758) increased with increasing levels of infection by a blood parasite, thus calling into question the reliability of hematocrit as an indicator of health and condition. Because hematocrit levels comprise both cell size and density, it is possible that high MCV or large cell size related to the quick release of immature cells in response to blood loss (Dein 1986) could result in an increased PCV rather than a lowered PCV as expected with blood loss.

In conclusion, our results indicate that condition-dependent mate choice or preference is employed by bushy-tailed woodrats. However, it is still uncertain whether females discriminate between males using odour alone, as is the

case with many small mammals. Preference trials that isolate odour from visual cues and a more long-term study are needed to resolve this issue.

Acknowledgments

We thank S. Gil and A. Dang for assistance in conducting field research and analyses. In addition, we thank R. Boonstra for use of laboratory facilities, technical advice, and helpful discussions regarding the results of our experiment. Research was conducted with funding from a Natural Sciences and Engineering Research Council of Canada grant awarded to J.S. Millar.

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