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The Influence of Reproductive Status on Foraging by Hoary Marmots (*Marmota caligata*)

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Summary. Predictions were made and tested, comparing the foraging behavior of reproductive (rf) and nonreproductive (nrf) female hoary marmots, with the following findings: In June, no differences occur between rf's and nrf's, regarding daytime foraging. However, rf's forage more in the evening and during inclement weather, suggesting that greater nutritional needs and higher reproductive value select for the assumption of more risk while foraging. These differences disappear by August, when nutritional needs and reproductive values of rf's and nrf's are comparable. Finally, rf's reduce their near-burrow foraging relative to nrf's, which minimizes competition with their own young.

Introduction

Although an evolutionary perspective seems most striking when directed toward the elucidation of complex social patterns (Wilson 1975), it should be at least equally valid when applied to relatively 'nonsocial' behaviors. In this manuscript, I discuss the results of four years of research testing evolutionarily based predictions concerning the foraging behavior of female hoary marmots, *Marmota caligata*.

Hirshfield and Tinkle (1975) defined reproductive effort as "the proportion of total energy, procured over a specified and biologically meaningful time interval, that an organism devotes to reproduction." Natural selection is expected to maximize the effective reproductive effort expended by any individual over the course of its lifetime. Reproductive *value*, by contrast, is a measure of the contribution of an individual to the next generation (Fisher 1930). Organisms are predicted to allocate resources at any given age so as to maximize their total reproductive value at that time. By so doing, each individual maximizes its fitness over its lifespan.

Although an increase in reproductive effort at any given age would normally lead to an increase in current reproductive value at that age, we can also anticipate a cost associated with such effort, which would reduce the residual reproductive value of the individual concerned. Depending on the ecological parameters of the species in question, variations will occur in the reproductive value of individuals at different stages in their life history. Accordingly, we can expect selection of favor different degrees of reproductive effort at different times (Williams 1966).

Trivers (1972) defined parental investment as "any investment by parents in offspring that increases the chances of the offspring's survival and hence reproduction at the cost of the parent's ability to invest in future offspring." As such, it differs from reproductive effort largely in that parental investment emphasizes behavior that is directed toward existing offspring. Foraging by a parent marmot constitutes parental investment when it takes place in a manner that either reduces the nutrient input of the parent or increases the predator risk suffered by the parent, or in some other manner reduces the parent's ability to invest in future offspring, in return for increasing the nutrient input of its offspring or reducing the predator risk suffered by the offspring, or in some other manner increasing the chances of the offspring's survivial and hence reproduction. Accordingly, parental marmots can be expected to show signs of parental investment not evident among comparable, adult animals who are nonparental.

The present study attempts to relate optimal foraging theory (Schoener 1971; Pyke et al. 1977), reproductive effort and life history strategies (Hirshfield and Tinkle 1975; Stearns 1976), and a predictive approach to sociobiology (Barash 1980), in which ani-

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Table 1. Composition and observation hours at study colonies

	Colony	Observa-hours	Adult males	Reproductive females	Infants	Nonreproductive females	Yearlings
1976	Granite	87	2	1	5	1	2
1976	Dickerman	90	1	1	3	0	0
1977	Granite	93	1	1	3	1	4
1977	Dickerman	84	1	0	0	1	1
1978	Bagley	85	1	1	4	0	1
1978	Goat	82	1	0	0	1	3
1979	Bagley	96	1	0	0	1	4
1979	Goat	88	1	1	3	0	0

mals are expected to behave in a manner that maximizes their inclusive fitness. Specifically, I shall attempt to evaluate several predictions based on the above, all of which imply consequences for the foraging behavior of hoary marmots.

Materials and Methods

Hoary marmots (*Marmota caligata*) inhabit talus slopes, sub-alpine and alpine meadows from central Alaska, the Yukon Territory, central and northern British Columbia, the Cascade Mountains of Washington and southern British Columbia, the Bitteroots of Idaho, the Rocky Mountains of northwest Montana, and the southern Rocky Mountains of Alberta (Howell 1915). The basic ecology and social organization of this species is only now being described (Barash 1974; Holmes 1979), although it appears to share many features with the somewhat better-known Olympic marmots (*M. olympus*) (Barash 1973), and the European Alpine marmots (*M. marmota*) (Barash 1976a).

Data for the present study were collected at three different geographic sites within the state of Washington: Mount Dickerman and Granite Mountain, two of the western peaks of the central Cascade range, near Snoqualmie Pass, at an elevation of about 1,900 m; and along the southwest flanks of Mount Baker, northern Cascades, at an elevation of about 1,800 m. Four different colonies were observed, each for two years; the composition and observation time at each is shown in Table 1.

Results

Like other high-altitude marmots, *M. caligata* appears to breed biennially – in alternate years (Barash 1974; Holmes 1979); or at least, it is common for adult females to skip a reproductive year. For present purposes, females producing infants during a given year will be termed 'reproductive females,' or rf's, as opposed to females that do not produce infants during that given year, termed 'nonreproductive females,' or nrf's. Each adult female was observed for one year as an rf and one year as an nrf. Copulations typically occur in early to mid-May, shortly after female emergence, with the young born in early to mid-June, after a gestation of about 30 days. The well-furred and ambulatory young typically first appear aboveground in July when about 3–4 weeks old, at which time weaning is well-advanced, if not complete.

Predictions

Accordingly, reproductive females in May and June have a higher reproductive value than do nonreproductive females at the same time. Given the metabolic demands of pregnancy and lactation, I predicted that rf's at this time would have greater foraging needs than would nrf's. However, as Westoby (1974) has pointed out, herbivores are generally limited by the rate at which they can process food in their gut rather than the rate of capture of nutrients, since they feed on immobile foods of low caloric density and must balance micronutrient intake as well. The typical foraging pattern for marmots is to feed in a series of bouts throughout the day, separated by within-burrow periods during which digestion is presumably occurring and individuals are relatively safe from predators.

I made the follwing specific predictions concerning foraging behavior of rf's and nrf's:

1) In June (during late pregancy and early lactation), rf's will run more risks than nrf's in order to meet their presumed greater foraging needs. In other words, rf's were predicted to increase their reproductive effort, at some possible cost to their residual reproductive value, when their present reproductive value is high relative to the present reproductive value of nrf's.

2) The difference in nutritional needs between rf's and nrf's would be less in August than in June. By August, even parental care is greatly reduced from July, since the infants are weaned and nutritionally – although not socially – independent. Furthermore, although rf's may be under selection for increased foraging to compensate for the costs of pregnancy and lactation just incurred (Barash 1976b), there is minimal difference in current reproductive value between rf's and nrf's at this time. This entire treatment differs greatly from that usually employed in studies of optimal foraging, in that both pursuit and handling time – typically considered as important in foraging models (Schoener 1971) – are essentially zero. Furthermore, this study identifies *risk* as a significant consideration in optimal foraging (for a more extensive treatment, see Holmes, unpublished work).

3) Because the fitness of rf's is largely dependent on the success of their infants, who themselves have

Table 2. Percentages of time foraging by reproductive and nonreproductive females during June and August

a) From 08.00 to 20.00 hours, including only fair, partly cloudy, and high overcast weather, and based on a minimum of 250 observation minutes per animal per month

	June	August
Reproductive females	28	34
Nonreproductive females	25	31

b) From 20.00 to 21.30 hours, again including only fair, partly cloudy, and high overcast weather, and based on a minimum of 50 observation minutes per animal per month

	June	August
Reproductive females	13	9
Nonreproductive females	4	11

c) From 08.00 to 20.00 hours, during fog, rain, or snow, based on a minimum of 50 observation minutes per animal per month

	June	August
Reproductive females	9	2
Nonreproductive females	3	3

their own nutritional needs via foraging, rf's can be predicted to modify their foraging so as to minimize competition with their infants, whereas comparable modification of nrf foraging should not occur.

Empirical Tests

I obtained a measure of foraging activity by censusing each adult female every 5 min and recording (with a stopwatch) the number of seconds spent foraging during the ensuing 1 min. By dividing the total number of seconds foraging by the total observation time, a foraging index was obtained – i.e., the percentage of time spent foraging by rf's and nrf's. To avoid possible bias in foraging percentage as a function of time of day, observation hours for rf's and nrf's were balanced during each hour interval ($\chi^2 = 1.04$; 11 *df*). Table 2a contrasts rf and nrf foraging activity between 08.00 and 20.00 hours in June and August, during fair, partly cloudy, or high overcast weather. Contrary to the prediction, there are no significant differences between these two classes of adult females. However, when foraging behaviors of rf's and nrf's are contrasted between 20.00 and 21.30 hours (by 21.30 hours, all marmots are belowground), rf foraging is significantly greater than that of nrf's in June but not in August (binomial test, $P < 0.05$; Table 2b). A comparable pattern appears when daytime foraging of rf's and nrf's between 08.00 and 20.00 hours is compared, considering here only days characterized by heavy fog, rain, or snow (binomial test, $P < 0.05$; Table 2c).

Table 3. Mean and standard deviation of distances of reproductive and nonreproductive females from the nearest burrow, in meters, during June and August (including only fair, partly cloudy, or high overcast weather and based on a minimum of 100 measurements per animal per month)

	June	August
Reproductive females	11 ± 3	7 ± 2
Nonreproductive females	5 ± 1	8 ± 2

Further evidence of early-season differences between rf's and nrf's in risk acceptance during foraging is provided by comparing the location of foraging. At 15-min intervals during both June and August, I indicated the position of rf's and nrf's on enlarged photographs of the study sites, and measured the distance from each animal to the nearest burrow. Predators upon marmots include cougars (*Felis concolor*), coyotes (*Canis latrans*), and golden eagles (*Aquila chrysaetos*). Marmots never fight a predator unless they are directly cornered and have no alternative; if they can, they retreat to a burrow. Accordingly, distance to the nearest burrow should be another measure of the risk incurred, with risk increasing approximately linearly with the distance. On the other hand, forage availability seems also to increase with greater distance from a burrow, as the depleting effects of foraging by other marmots is felt less strongly (Holmes 1979). During June, rf's feed significantly farther from the nearest burrow than do nrf's (*t*-test, $P < 0.05$, Table 3), consistent with the expectation that they will run greater risks when experiencing greater need, while in August, the differences are once again not significant (Table 3).

As expected, rf's tend to give more alarm calls than do nrf's, they spend more of their nonforaging time close to their burrows, and while close to their burrows, they look up more often than do nrf's (Table 4). However, despite their greater proximity to their burrows, the foraging intensity of rf's near their natal burrows is less than that of nrf's near *their* home burrows. I placed wooden stakes at measured distances from both natal burrows and the burrows of nonreproductive females, so that rf's and nrf's could be assigned to one of three concentric rings: less than 5 mm from the burrow, between 5 and 15 m from the burrow, and greater than 15 m. Hoary marmot infants typically emerge from their burrows during the second to third weeks in July – during July, I scan-censused rf's and nrf's every 5 min, assigned them to one of the three distances from their burrows, and then obtained a foraging percentage for each

Table 4. Reproductive versus nonreproductive female alarm calling, burrow proximity, and looking-up times during July and August (mean ± SD)

	Alarm-calling (per female per hour)	Burrow proximity (% of 5-min censuses within 5 m of home burrow)	Looking-up time (per minute per animal)
Reproductive female	0.80 ± 0.3	45	21 ± 5
Nonreproductive female	0.33 ± 0.2 $P < 0.05$ (*t*-test)	21 $P < 0.05$ (binomial test)	11 ± 3 $P < 0.05$ (*t*-test)

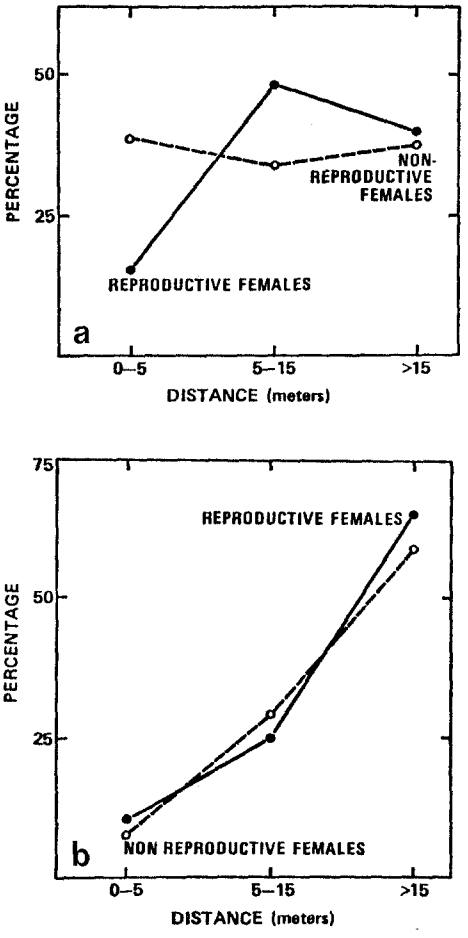

Fig. 1. a The percentage of all recorded foraging times during July at which reproductive and nonreproductive females were within different distances of their home burrows (based on a minimum of 50 observation minutes within each distance interval per animal); **b** presents comparable data for August

case, using the same procedure as described above. Again, the hourly observation regime was comparable for rf's and nrf's ($\chi^2 = 0.44$, 11 *df*). The results (Fig. 1 a and b) show that rf's conduct significantly less of their foraging within 5 m of their burrows than do nrf's ($P < 0.05$; binomial test). The opposite is true for 5–15 m of their burrows ($P < 0.05$; binomial test). Beyond 15 m, no differences are apparent. This tendency for rf's to forage less near their burrows than nrf's do near theirs is especially striking in view of the greater proportion of nonforaging time rf's normally spend near their burrows. Thus, whereas nrf's averaged 22% of their census time during July within 5 m of their burrows, rf's averaged 43% ($P < 0.05$; binomial test).

Discussion

I interpret these results as follows: both rf's and nrf's are under pressure to forage substantially, since they are limited to an aboveground vegetative growing season of only about four months, during which they must accumulate sufficient nutrients to last an entire 12 months. Both rf's and nrf's therefore forage at a high level during most days, probably at the maximum that permits effective gut absorption – hence, the data of Table 2a. However, during June, when their current reproductive value is higher than that of nrf's, rf's accept higher risks in order to obtain the needed nutrient – this increased foraging risk can therefore be considered a form of reproductive effort, with costs incurred via the likelihood of increased predation as well as possible increased risks of hypothermia. Both of these are presumably more significant as risks after 20.00 hours and during inclement weather (Table 2b and c).

I interpret the reduced near-burrow foraging of rf's relative to nrf's (Table 3) as avoidance of food competition and, hence, a form of parental investment, in that rf's must travel farther from their burrows, expending time and energy in the process, while also being presumably at greater risk from predators. As a proximate mechanism, rf's might show reduced near-burrow foraging because they are more preoccupied with their infants, including greater watchfulness vis-à-vis predators. However, when I reanalyzed the data from Figure 1 a, comparing rf data when the infants were belowground with those obtained when the infants were aboveground, there was no significant difference in the results ($\chi^2 = 2.2$; 2 *df*). Conceivably, reduced near-burrow foraging by rf's could also reflect a somewhat different maternal strategy from that suggested here: it could serve to allow plant growth that provides additional cover for the infants. In addition, since forage availability increases at increased distance from occupied burrows, rf's who concentrate their foraging at greater distances may actually be receiving a greater immediate nutritional

return. However, this is consistent with the arguments presented above, since the risks incurred by these rf's is presumably greater, just as their likely need for nutritional return is also greater than for nrf's. This could operate along with reduction in forage competition with their own infants to predispose rf's to forage at a greater distance than nrf's. In addition, the near-burrow, far-from-burrow differential in forage availability is actually greater in August than in July, by which time reproductive females are no longer avoiding near-burrow foraging and, of course, their infants are wandering widely. Given my present data, however, I cannot separate these two considerations. In any event, these foraging differences between rf's and nrf's disappeared by August (Fig. 1b). By this time, the infants are wandering far from their natal burrows and therefore presumably reduce the pressures on rf's to avoid near-burrow foraging. In addition, the nutritional differences between rf's and nrf's are presumably reduced by August, thereby mitigating against differential far-from-burrow foraging by rf's, while furthermore, meadow desiccation by August generally seems to result in more selective foraging and hence greater wandering by all animals.

The foregoing treatment assumed that some degree of forage competition occurs among marmots, such that by foraging in the immediate proximity of an infant, an adult reduces the quality and/or quantity of forage available to that infant. This seems likely, especially since for the first several weeks after their emergence, infants restrict their activities to within several meters of their natal burrows, only gradually expanding their range to encompass that occupied by older colony residents. Woods (1973) found significant differences in the standing crop biomass between enclosed and open plots in meadows grazed by Olympic marmots, although he did not analyze these differences in terms of the location of the enclosures relative to refuge burrows. Furthermore, to my knowledge, no studies to date have directly assessed forage depletion as a function of age-specific utilization of a particular meadow area. Therefore, the following research may be suggestive, but must nonetheless be considered tentative, pending documentation of actual forage competition in these animals. On the other hand, forage availability is almost certainly crucial to these animals. Armitage and his students (1976) have shown that 50% of first-year yellow-bellied marmots will die during their first winter, presumably due to insufficient fat reserves.

Further studies linking reproductive strategies and such apparently nonsocial behaviors as foraging ought to help solidify the application of evolutionary principles to other aspects of animal behavior.

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