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Mate Guarding and Gallivanting by Male Hoary Marmots (*Marmota caligata*)

David P. Barash
Animal Behavior Program, Departments of Psychology and Zoology, University of Washington, Seattle, Washington 98195, USA

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Summary. Seven years data on the vernal behavior of hoary marmots, *Marmota caligata,* suggest that males engage in a two-part reproductive strategy, which consists of guarding their mates against possible copulation with additional males, and also gallivanting – wandering about in search of additional reproductive opportunities for themselves. Data are presented which support seven predictions derived from the assumption that mate guarding and gallivanting are parts of a reproductive strategy by male marmots.

Introduction

Because of male-female differences in the pattern of parental investment (Trivers 1972), male-female differences in reproductive strategies can be expected, with males typically selected to be sexually aggressive and competitive in contrast to females which tend to be relatively coy and evaluating (Williams 1966). This predicted difference in strategies occurs in large part because an additional copulation with a new individual is more likely to enhance male fitness than female fitness. In addition, and especially in cases of male parental investment and/or monogamy, male fitness is liable to be reduced directly by successful out-of-pair-bond copulations on the part of the mated female. As a result, males can be expected to partake of a two-part mating strategy: guard their female(s) against copulation with other males, and also seek extra copulations for themselves, even with already-mated females if necessary. This pattern has recently been reported for birds; the present communication describes a comparable phenomenon in a mammal, the hoary marmot, *Marmota caligata.*

The data presented here were obtained in the course of long-term field studies on this species. An account of mixed male strategies in bank swallows (Beecher and Beecher 1979) influenced me to make the predictions described below and then to test them with existing data from 1974 to 1979; when preliminary analysis supported these predictions, I obtained additional data during summer, 1980, with the mixed male strategy specifically in mind. The years 1974 to 1980 are combined in the following account.

Mate guarding may be defined as behavior by one member of a mated pair, by which the guarding individual behaves in a manner which directly reduces the probability that the guarded individual will copulate with another animal. Hence, mate guarding should be distinguishable from simple sexual association in that mate guarding should be directly correlated with the probability of cuckoldry rather than with sexual opportunities for the guarding individual per se. Webster's New World Dictionary defines gallivant as "go about in search of adventure or excitement"; it has distinctly sexual overtones. Gallivanting behavior has already been described and the term introduced into the professional literature, in a previous study of the Olympic marmot (Barash 1973), when individuals were seen to make forays beyond the normal confines of their colony area, presumably in search of reproductive opportunities. Hence, gallivanting should be directly correlated with the probability of achieving additional copulations for the gallivanter. For this study, I arbitrarily defined a gallivant as any excursion of more than 100 m from the home burrow; at present, data are unavailable by which to determine 95% confidence ellipses or other patterns of spatial use for marmots. However, field experience suggests that excursions of 100 m or more are sufficiently unusual to warrant special attention.

Marmots are fertile only during the first few weeks following emergence from hibernation. Young of the year emerge in late July, following about 30 days gestation and another 30 days for the animals to become fully-furred, open-eyed and ambulatory; this chronology places insemination at late May, about two weeks

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post-emergence. Furthermore, females trapped at that time have swollen vaginas, not apparent by mid-June, and they also show a characteristic syndrome of estrus behavior, not found at other times. A similar pattern has been found for yellow-bellied (Armitage 1965) and Olympic marmots (Barash 1973).

Assuming that mate-guarding and gallivanting are male reproductive strategies in hoary marmots, then the following general predictions were made:

1. Gallivanting will be overwhelmingly a male phenomenon; gallivanters will be repulsed by colony males; and gallivanters will seek sexual access to females.

2. Mate-guarding will be more prominent early in the year, when females are fertile, than later when they are infertile.

3. At the same time of year, mate-guarding will be more prominent when the physical location of females renders them more likely to cuckold the colony male.

4. Males will initiate and seek to maintain proximity to females more than vice versa.

5. Group-living males will mate-guard more than monogamous males, since they are at greater risk of being cuckolded.

6. Males whose females are nonreproductive during a given year will mate-guard less and gallivant more whereas males whose females are reproductive during a given year will mateguard more and gallivant less.

7. Among group-living males, the frequency of gallivanting will vary inversely with the proportion of neighboring males and directly with the proportion of neighboring females.

Materials and Methods

Hoary marmots are large, terrestrial sciurid rodents that inhabit subalpine and alpine meadows, and talus slopes in the northern Rocky Mountains, the Cascades, and the mountains of British Columbia north through Alaska (Howell 1915). Their basic sociobiology resembles that of the Olympic marmot, *M. olympus* (Barash 1973), in that they are either monogamous (Holmes 1979) or mildly polygynous, and within-colony interactions tend to be socially tolerant (Barash 1974). Transient individuals are only rarely observed, and adult males are easily categorized as either colony males (associated with one or more females) or peripherals (residing near another male and his female(s), but clearly subordinate to the colony male). A similar pattern has been described for yellow-bellied marmots, *M. flaviventris* (Armitage 1974). The behavior of peripheral males is currently under study; except where specified, data in the present report are only for colony males. Of particular interest to this report is the fact that some colony males are geographically isolated and reside monogamously with a single female; these males do not typically interact with additional adults. By contrast, other males live in complex arrangements in which several females and additional males (both peripheral and colony) are nearby. These latter individuals interact frequently (Barash 1975).

Colony males experiencing these extended, multi-male arrangements may or may not be polygynous. In this report they will be called group-living as distinct from isolated monogamists. All identified adult females were associated with either a monogamous or a group-living male. Data for this report represent 689 observation hours conducted during the first six weeks following emergence from hibernation, between mid-May and the end of June, from 1974 through 1980. 376 observation hours were gathered on five different monogamous sites and 313 h on four different group-living sites, located on the northeast ridges of Mount Baker, two km northeast of Cayuse Pass, and at Paradise, in Mount Rainier National Park, all in the state of Washington. The four group-living sites comprised a total of ten adult males and 14 adult females; combined with the five monogamous sites, this report therefore presents data obtained from 15 different adult males and 19 different adult females.

Results

Prediction 1. Males performed 146 out of 150 observed gallivants. In all 41 cases in which gallivanters were observed after entering a new colony containing an adult male, the gallivanter was repulsed by the colony male. In all these cases, the gallivanter retreated immediately (within 5 s) after encountering the colony male. This typical response of an intruder to a territorial resident is well-known to ethologists, and suggests that both gallivanter and guarder are abiding by "bourgeois" strategies (Maynard Smith 1976). In any event, the cost incurred by a gallivanter who encounters a resident appears to be low, since no extensive fights resulted.

Two different colony males were live-trapped and removed from their colonies on two successive days each. Seven adult males were observed to gallivant at these colonies while the colony male was in captivity: in one case the gallivanter was repulsed by a non-breeding adult female, in one case the gallivanter entered a burrow with an estrus female, in two cases the gallivanter copulated above-ground with estrus females, and in the remaining three cases the gallivanter associated with the resident females although they were lost to view before any outcome could be ascertained.

The observed gallivanting rates, per animal per hour, are as follows for monogamous and group-living males combined: – weeks 1–3:0.21 (SD 0.17); weeks 4–6:0.12 (SD 0.08); weeks 7–9:0.

Prediction 2. Colony males were censussed every 10 min, and their distance to the nearest adult female was recorded as less than 5 m greater than 5 m, or unknown. The results (Table 1a) show that for both monogamous and group-living males, male-female distance increased significantly during the season. Thus, the average number of occasions when male-female distances were less than five meters declinded significantly (for both monogamous and group-living males) from weeks 1–3 to weeks 4–6. By contrast, there was no change in the number of occasions when male-female distances exceeded five meters.

Table 1. a Recorded male-female distances, per male per observation hour. **b** Number of departures clearly initiated by individuals of either sex. **c** Responses of both males and females to departures by the other sex. Based on 613 observation hours on 15 different males in each case, with a minimum of 40 h and 3 different males in each category. Data are presented as means, with SD's in parentheses; *ns* no significance; * = $P < 0.05$; ** = $P < 0.01$; Mann Whitney U Tests

a	Less than 5 m		Greater than 5 m	
	Weeks 1–3	Weeks 4–6	Weeks 1–3	Weeks 4–6
Monogamous	0.70 (0.3) → * ← 0.36 (0.2)		1.2 (0.7) → ns ← 1.9 (0.6)	
	↓ **	↓ ns	↓ ns	↓ ns
	↑	↑	↑	↑
Group-living	1.88 (0.4) → ** ← 0.33 (0.2)		1.0 (0.8) → ns ← 1.4 (0.3)	

b	Monogamous		Group-living	
	Weeks 1–3	Weeks 4–6	Weeks 1–3	Weeks 4–6
Female departed	0.47 (0.2) → ns ← 0.38 (0.3)		0.56 (0.3) → ns ← 0.41 (0.3)	
	↓ *	↓ ns	↓ **	↓ ns
	↑	↑	↑	↑
Male departed	0.18 (0.1) → * ← 0.40 (0.2)		→ ** ← 0.53 (0.3)	

c	Monogamous		Group-living	
	Weeks 1–3	Weeks 4–6	Weeks 1–3	Weeks 4–6
Female followed male	0.03 (0.02) → ns ← 0.02 (0.02)		0.08 (0.01) → ns ← 0.04 (0.03)	
	↓ *	↓ ns	↓ *	↓ ns
	↑	↑	↑	↑
Male followed female	0.29 (0.1) → * ← 0.08 (0.1)		0.55 (0.2) → * ← 0.1(0.1)	

Whenever male and female were within five meters and one of them walked away, the sex of the departing individual was also recorded when known. The results (Table 1b) show that:

a) Early in the season, females departed from males significantly more often than males departed females – with no difference between monogamous and group-living females in this respect, and

b) Later in the season, this pattern disappeared such that males and females did not differ in their frequency of departures. The response of males and females to departure by the other was also recorded.

The results (Table 1c) show that:

a) Early in the season, males were significantly more likely to follow departing females than females were to follow departing males, and

b) This pattern occurred early in the season, but disappeared later, due to changes in male behavior only.

Prediction 3. The likelihood of a female cuckolding her mate should increase in direct proportion to her distance from her home burrow at any given time, since this increases her proximity to neighboring males and also reduces the probability of the colony male intercepting any gallivanting neighbor male. Accordingly, mate-guarding is predicted in direct proportion to female distance from her home burrow. Based on 10-min scan samples, cases in which colony male-female proximity was less than five meters were categorized as to the distance of the female from her residence burrow at the time – less than 25 m or greater than 25 m. The results (Table 2) show that:

a) During weeks 1–3, both monogamous and group-living males attend their females more closely when females are beyond 25 meters from their residence burrow than when they are within 25 meters, and

b) These differences disappear by weeks 4–6 – providing further support for Prediction 2 as well. The tendency of colony males to attend females that are distant from their residence burrows and to do so early in the season is highlighted by the fact that on eight occasions, males made conspicuous runs across the colony, to within five meters of the female, apparently when they became suddenly aware of the female's location. On seven of these eight occasions, the female was more than 25 m from her residence

Table 2. Percentage of observations in which male-female distances were less than 5 m, as a function of the female's distance from her residence burrow. Based on 613 observation hours on 15 different males, with a minimum of 40 h and 3 males in each category. *ns* no significance; $*=P<0.05$, binomial test for difference in proportion

	Weeks 1–3		Weeks 4–6	
	Female 25 m	Female 25 m	Female 25 m	Female 25 m
Monogamous	36	→ * ← 60	17	→ns← 28
	↓	↓	↓	↓
	ns	ns	ns	ns
	↑	↑	↑	↑
Group-living	49	→ * ← 81	11	→ns← 16

burrow, and all eight of these instances took place during the first three weeks after emergence. Females were seen to enter a burrow 124 times while males were above-ground; comparable observations for males were made only five times.

Prediction 4. Males have already been shown to depart from females less than *vice versa* during weeks 1–3 (Table 1 b). Males also followed departing females more than females followed departing males (Table 1 c).

Prediction 5. During weeks 1–3, group-living males were closer to their females than were monogamous males; this difference had disappeared by weeks 4–6 (Table 1 a). Group-living males were also less likely to depart from females early in the season than were monogamous males (Table 1 b), and they followed departing females significantly more than did monogamous males (Table 1 c). Surprisingly, group-living males are not significantly more likely than monogamous males to guard a female who is far from her residence burrow (Table 2), although the difference is in the predicted direction.

The location of the nearest adult female was recorded when males began 31 different gallivants. For group-living males, 4 of 17 gallivants were initiated when the nearest adult female was out of her burrow: hence, 13 of the 17 gallivants by group-living males occurred while the nearest female was in a burrow. For monogamous males, 10 of 14 gallivants occurred when the nearest female was out of her burrow, and only four occurred when she was in a burrow. This difference fails to reach statistical significance (binomial test for difference of proportions), but the trend of these data nonetheless suggest that monogamous males are more likely than group-living males to go gallivanting when their female is out of her burrow.

Prediction 6. Since hoary marmots reproduce in alternate years, approximately half the females are nonfertile during any given year. Accordingly, half the females are therefore fertile during any given year, so the benefits of gallivanting should remain approximately constant. However, the costs should vary directly with the fertility of the already-mated females: a male whose female is nonfertile cannot be cuckolded. Group-living males are often polygynous; therefore, at least one of their females is typically fertile during any given year. Hence, Prediction 5 cannot crisply be tested with them. However, monogamous males are affiliated with either a fertile or nonfertile female each year. The gallivanting rate, per male per observation hour, during weeks 1–3, was 0.26 for group-living colony males, 0.19 for group-living peripheral males and 0.21 for monogamous males. These differences are not significant (Kurskal-Wallis one-way Anova). However, these are combined data for all monogamous males, regardless of the reproductive status of their female. Data on gallivanting rates are available for nine monogamous males, each of whom was associated with a female of known reproductive status: Four with fertile females, and five with non-fertile females.

The data (Table 3) show that:

a) Monogamous males paired with fertile females gallivanted less during weeks 1–3 than did monogamous males paired with infertile females, and

b) This difference disappeared by weeks 4–6.

Similarly, data indicative of mate guarding (spatial proximity, extracted from Table 1 a and presented in Table 4), show that:

a) Monogamous males paired with fertile females maintained greater proximity to their female during weeks 1–3 than do similar males paired with nonfertile females, and

b) This difference disappeared by weeks 4–6.

Prediction 7. Group-living males may be characterized by the sex of their adult neighbors. An index of the adult neighbor sex ratio (ansr) can be obtained by constructing a circle with radius of 100 m using the residence burrow of each focal male as the center, and recording the sex of all other adults whose residence burrows occur within the arbitrarily-defined circe. Data were obtained in this manner for eight different males during various times throughout the six-year period of this study; ansr's for three males were recorded in two consecutive years, and one male's ansr was obtained for three years, yielding a total of 17 marmot-years ansr data, of these, five cases yielded a male/female ansr exceeding 1.5, eight were between 1.5 and 0.5, and four were less than

Table 3. Gallivanting rate per animal per h, of monogamous males as a function of whether their females were fertile or non-fertile. Based on 149 observation hours, with a minimum of 20 h and 2 males in each category. *ns* no significance; $*=P<0.05$, Mann-Whitney U test

	Weeks 1–3	Weeks 4–6
Female non-fertile	0.46 (0.3) → * ←	0.20 (0.2)
	↓ * ↑	↓ ns ↑
Female fertile	0.10 (0.04) → ns ←	0.16 (0.03)

Table 4. Recorded male-female distances per male per observation hour, comparing monogamous males whose females were fertile with monogamous males whose females were non-fertile. Based on 149 observation hours, with a minimum of 20 h and 2 males in each category. *ns* no significance; $*=P<0.05$, Mann-Whitney U test

	Less than 5 m		Greater than 5 m	
	Weeks 1–3	Weeks 4–6	Weeks 1–3	Weeks 4–6
Female non-fertile	0.9 (0.4) → ns ←	1.1 (0.4)	1.4 (0.7) → ns ←	2.0 (0.6)
	↓ * ↑	↓ ns ↑	↓ ns ↑	↓ ns ↑
Female fertile	2.6 (0.4) → * ←	0.8 (0.5)	2.0 (1.0) → * ←	1.5 (0.6)

0.5. In the first series, the focal male had a high ratio of neighboring males to females, the second was intermediate and the third, a high ratio of neighboring females to males. The data on gallivanting rates show significant differences, in the direction predicted i.e., gallivanting rates varied inversely with the ansr. Thus, the per capita gallivanting rates were as follows (SD in parentheses): ansr greater than 1.5-0.14 (0.02); ansr 1.5-0.5-0.30 (0.02); and ansr less than 0.5-0.56 (0.1). This is based on 174 observation hours, with a minimum of four males and 35 h in each category. The differences are significant at $P<0.05$, Kruskal-Wallis one-way analysis of variance.

Discussion

These data are consistent with the above predictions and support the hypothesis that male behavior involves a combination of mate guarding, in which males seek to defend and enhance their probability of paternity with mated females, and gallivanting, in which males seek to achieve copulations with additional females while also minimizing the probability that they will be cuckolded.

It seems most parsimonious to interpret gallivanting as part of the males' reproductive strategy, with the ultimate reproductive pay-off occurring with low frequency, but nonetheless great import. Among alternative interpretations for gallivanting, it seems unlikely that gallivanters are simply seeking additional forage, since

1. females should be no less motivated in this regard than males, and
2. gallivanters conspicuously approach other colonies rather than potential foraging sites. Gallivanters may also be assessing the possibilities of taking over new colony sites, a likely opportunity if a nearby resident colony male has died during hibernation. However, this hypothesis might predict constant gallivanting rates throughout the season, with perhaps a slightly higher frequency immediately after emergence from hibernation. On the other hand, the observed seasonal decline in gallivanting frequency is also consistent with the hypothesis that gallivanters are seeking new colony sites, if males learn early that potential space is already occupied and therefore, they cease gallivanting. I have never observed a colony male to adopt a new colony; hence, I believe that gallivanters are not seeking new colony sites. The possibility remains, however, that to some extent, gallivanting males are both seeking copulations and exploring for new locations.

Insofar as gallivanting is influenced by both factors, we might predict that peripheral males should gallivant more than colony males, since the former have not yet obtained a colony residence whereas the latter have. However, similar results would be predicted if gallivanters are simply following a mating strategy, since under that assumption, colony males would also gallivant less than peripherals – not because they are less motivated to seek new residences, but rather because they are more in danger of being cuckolded, and hence, are more likely to engage in mate-guarding.

Although mate guarding and gallivanting are best seen as an integrated reproductive strategy of males, these behaviors are necessarily mutually exclusive at any one time: a guarding male cannot simultaneously be gallivanting, and vice versa. In arriving at his reproductive strategy, each male should be selected to consider the immediate local situation, especially the reproductive state of his female(s) and the adult neighbor sex ratio. With sufficient data on costs and benefits of the various alternatives, an appropriate analysis may well parallel that of game theoretic models, solving for an evolutionarily stable strategy (Maynard Smith 1976) since the pay-off to each participant seems likely to vary with what the others are doing.

Moreover, such pay-offs may well be frequency dependent. Consider a hypothetical population composed only of mate-guarders: Since marmots tend toward polygyny, some females would be unguarded even in a population of guarders. This in itself would render the population susceptible to invasion by gallivanters. Furthermore, if all other males are guarding, then a gallivanting male would not suffer the possible cost of being cuckolded by another gallivanter. As gallivanting spread, however, it would become increasingly costly, until an equilibrium is reached. This equilibrium would depend on many additional social and ecologial factors, as well as the degree of panmixis (Schwartz and Armitage 1980).

Initial efforts to model ESS systems of this sort have recently been made (Rubenstein 1980), although the necessary field data are still lacking. In particular, there is great need for data on the reproductive success of gallivanters and mate-guarders. The existence of alternative behavioral strategies suggests the existence of evolutionary stability, but this remains hypothetical unless the fitness of both strategists is shown to be equal. Although it is possible that peripheral males are following a pure strategy (gallivant only, since they have no females to guard), colony males are more likely engaging in a mixed, conditional strategy – guard if your female(s) are reproductive and/or if the adult neighbor sex ration is high, gallivant if your female(s) are nonreproductive and/or if the adult neighbor sex ratio is low. It seems unlikely, however, that peripheral and colony males represent an ESS, since the reproductive success of the former appears to be low, although convincing data on this point are not yet available. If peripheral males are younger than colony males, as seems likely, then in all probability some of the former ultimately accede to the status of the latter, as colony males die or become moribund. This remains to be confirmed.

In addition, there are numerous currently unevaluated complications for the evolution of mate guarding and gallivanting behavior, and for our understanding of them. For example, there may be possible costs due to increased liability of predation. Thus, the typical marmot response to a predator's appearance is to enter a burrow. Being away from his home area, a gallivanter may be more conspicuous to would-be predators, less familar with the location of refuge burrows, and also farther from such burrows, which tend to be concentrated in residence meadows. In addition, gallivanting males may increase the risk to predation of their females and offspring, since while gallivanting, males are not available to spot predators and give alarm calls; this might be especially important at monogamous sites, where no additional adults are available to sound an alarm. Finally, a male's confidence of paternity might be expected to influence his tendencies to mate guard or gallivant; this should once again be more consequential at monogamous than at group sites.

To some extent, concern with alternative mating strategies is male chauvinist in approach, insofar as it focuses on the various strategies of males and assumes that females are equally seducible by all males. This approach seems legitimate, up to a point, since the dramatic behavioral phenomena in question are performed by males – in the present case, guard or gallivant. However, sociobiologic theory also allows for substantial female choice, as well as female manipulation of male sexual behavior (e.g. Cox and LeBoeuf 1977). A more inclusive theory of alternative mating strategies must therefore consider the role of females as well. This is another goal for future work.

In his now classic treatment of parental investment theory, Trivers suggested that even in monogamous species, males would be selected to follow a mixed reproductive strategy, providing paternal investment as needed while also not passing up opportunities to mate with additional females, who would not be aided. Among most mammals – including marmots – monogamy is rare and males have little to contribute directly to their offspring. However, in such cases, a mixed reproductive strategy seems nonetheless indicated, with males selected both to guard their mate(s) and to solicit additional copulations. This pattern – a sexual double standard – has been widely remarked among *Homo sapiens* (Broude and Greene 1976). It appears to be significant among certain non-human mammals as well, and indeed, it may well prove to be the rule rather than the exception.

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