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Litter relocation behavior in two species of ground-dwelling squirrels

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Abstract

Maternal investment in mammals may take many forms, including spatial relocation of offspring. Litter relocation behavior, in which a female moves her litter to a new location, has been reported for several species of carnivores and rodents but has received little study. We describe litter relocations during long-term studies of two species of ground-dwelling squirrels, yellow-bellied marmots (YBM, *Marmota flaviventer*) and golden-mantled ground squirrels (GMGS, *Callospermophilus lateralis*), to determine the distance and frequency of litter relocations and to explore possible explanations for litter relocation behavior. We observed 19 litters relocated by YBM mothers and 32 by GMGS mothers. Although YBM are much larger than GMGS, relocation distances for YBM (median = 46 m and range = 15–324 m) were not greater than those for GMGS (median = 79 m and range = 16–252 m), possibly because YBM home ranges in our study area were exceptionally small. Frequency of litter relocation was greater for GMGS (21% of litters produced) than for YBM (10%), perhaps because GMGS experience fewer social constraints or greater predation risk. We identified several possible costs (energy expenditure and vulnerability to predators while transporting young) and benefits (reduced exposure to predation risk, increased habitat quality, and social benefits) of litter relocation. Future studies should continue to explore litter relocations to better understand the ecological causes and consequences of this behavior.

KEYWORDS
animal movement, *Callospermophilus lateralis*, *Marmota flaviventer*, predation risk, reproductive behavior, space use

1 | INTRODUCTION

Maternal care in mammals is characterized by post-partum investment in the form of lactation, which is energetically expensive (Clutton-Brock, 2016). In addition, maternal investment may occur post-weaning, often in the form of antipredator behaviors such as vigilance for early detection of predators (Caro, 1987; Costelloe & Rubenstein, 2018), alarm calling to warn offspring of danger (Wilson-Henjum, Job, McKenna, Shannon, & Wittemyer, 2019), or hiding young to minimize predator detection (Fisher, Blomberg, & Owens, 2002; Lent, 1974). Mothers may also invest in their offspring through spatial relocation. For instance, reproductive females will sometimes move away from the natal site to a new location, bequeathing their burrow or territory to their offspring (Harris & Murie, 1984; Price & Boutin, 1993). In other cases, females will relocate their litter from the natal site to a new location, presumably where fitness benefits are perceived to be greater (Coulon, Graziani, Allaine, Bel, & Pouderoux, 1995; Swaisgood, Owings, & Rowe, 1999).

Litter relocation behavior has been reported in a variety of carnivore species, including gray wolves (*Canis lupus*; Ausband et al., 2016), cheetahs (*Acinonyx jubatus;* Laurenson, 1993), pine martens (*Martes martes*; Kleef & Tydeman, 2009), and spotted hyenas

(*Crocuta crocuta*; Boydston, Kapheim, & Holekamp, 2006). It has also been reported in some rodents, such as deer mice (*Peromyscus maniculatus*; Sharpe & Millar, 1990), red squirrels (*Tamiasciurus hudsonicus*; Kerr & Descamps, 2008), alpine marmots (*Marmota marmota*; Coulon et al., 1995), and California ground squirrels (*Spermophilus beechyi*; Hennessy & Owings, 1988; Swaisgood et al., 1999). Litter relocation seemingly is costly for the female because of increased exposure to predation while carrying offspring. In addition, females likely expend extra energy during transit by carrying pups individually and shuttling back and forth between locations (Pero, 2015). Although very little is known about the evolutionary significance of litter relocation behavior (Kerr & Descamps, 2008), females may benefit by moving their offspring to reduce predation risk in circumstances where predator activity around the natal site is high (Kerr & Descamps, 2008; Kleef & Tydeman, 2009; Swaisgood et al., 1999) or to increase habitat quality in cases where neighboring habitat is of higher quality than that surrounding the natal site (Pero, 2015). Other proposed benefits include avoiding or reducing ectoparasite infestation (Pero, 2015; Roper, Jackson, Conradt, & Bennett, 2002), escaping the threat of infanticide (Ebensperger & Blumstein, 2007), promoting integration of pups into social groups (Boydston et al., 2006), or evading adverse abiotic conditions (Ausband et al., 2016). However, information on litter relocations is largely anecdotal, with documentation of litter moves and potential causal factors available for only a few species (Ausband et al., 2016; Boydston et al., 2006; Pero, 2015), perhaps due to the infeasibility of predicting when and where relocation events will take place.

We observed multiple litter relocations during long-term studies of two ground-dwelling squirrels: the large-bodied (2,560–3,880 g) yellow-bellied marmot (YBM; *Marmota flaviventer*), and the small-bodied (130–230 g) golden-mantled ground squirrel (GMGS; *Callospermophilus lateralis*) (Armitage, 1981). Prior accounts of litter relocations of YBM and GMGS are limited to one report, for GMGS (Huestis, 1947). Here, we provide photographic documentation and a detailed description of litter moves to characterize the frequency and distance of litter relocations in both species and to explore possible explanations for litter relocation behavior.

2 | METHODS

Our study took place at the Rocky Mountain Biological Laboratory in the East River Valley, Gunnison County, Colorado (38°57′N, 106°59′W) at an altitude of 2,900 m. Long-term studies of YBM (Armitage, 2010; Blumstein, 2013) and GMGS (Wells & Van Vuren, 2018) have been conducted at this location since 1962 and 1990, respectively. Common predators in this region include coyotes (*Canis latrans*), red foxes (*Vulpes vulpes*), long-tailed weasels (*Mustela frenata*), and short-tailed weasels (*Mustela erminea*) (Kneip, Van Vuren, Hostetler, & Oli, 2011; Van Vuren, 2001). Female YBM typically live in colonies, located at discrete habitat patches surrounded by unsuitable habitat (Armitage, 2014), although some females are solitary (Downhower & Armitage, 1971). Colonies are spatially fixed and have been occupied continuously for over 50 years (Blumstein, 2013). Colonies consist of one or more matrilines; home range overlap is extensive within a matriline, but it is minimal or non-existent between matrilines (Armitage, 1991). Female GMGS are solitary, although they often live in close proximity to conspecific neighbors (Wells & Van Vuren, 2017). For both species, females give birth in the natal burrow, where they nurse their pups for 25–30 days before the pups emerge and begin feeding on their own (Armitage, 1981; Wells & Van Vuren, 2018).

Each year, individuals of both species were trapped and marked, and pups were trapped upon emergence from their natal burrow. Intensive behavioral observations were conducted at four colonies for YBM (Armitage, 1974) and throughout a 13-ha study area for GMGS (Wells & Van Vuren, 2018). All procedures followed guidelines of the American Society of Mammalogists (Sikes & Animal Care and Use Committee of the American Society of Mammalogists, 2016) and were approved by the Institutional Animal Care and Use Committees of the University of Kansas, University of California, Davis, and Rocky Mountain Biological Laboratory.

Litter relocations were observed opportunistically. Relocation events were recorded during 1965–1996 for YBM and during 1995–2018 for GMGS, and we restricted our analyses for each species to those time periods. In all but 11 cases (five GMGS and six YBM), litter relocations were identified while in progress based on observations of a mother carrying one or more pups away from the home burrow. In the 11 cases, litter relocations were identified based on the abrupt change in location between burrows of a mother and her entire litter. We recorded litter size and relocation distance, the Euclidean distance between the former burrow and the new burrow. We also calculated total distance for the mother by multiplying the relocation distance by the number of trips required to move the entire litter (following Pero, 2015). Total distance moved by the mother was used as a proxy for the relative energy expenditure for relocating a litter. We then further categorized relocations as either "internal" moves or "external" moves. Relocation events that took place within a YBM colony, or within the home range of the GMGS mother (as defined by locations where the mother had been recorded prior to the event), were considered to be internal moves, while all other moves were considered to be external. Spatial ecology scales with body size (Jetz, Carbone, Fulford, & Brown, 2004), so we used Mann–Whitney U tests to compare relocation distances between species, based on the expectation that distances would be greater for YBM than for GMGS. In the event that a female moved her litter more than once either within or between years, we calculated the mean relocation distance for that female and used this composite value for analysis. We calculated frequency of litter relocations by comparing number of litters moved to total litters produced for each species throughout the study period. We assessed the potential influence of energetic cost on litter relocation behavior in two ways. To determine whether energetic cost influenced the likelihood of moving a litter, we compared the size of relocated litters to the long-term mean litter size for the GMGS (4.8 pups; Kneip et al., 2011) and YBM (4.1 pups; Schwartz, Armitage, & Vuren, 1998) populations we studied. To determine whether the energetic cost associated with moving larger litters influenced relocation distance, we calculated Spearman's rank correlation coefficients to determine whether relocation distance declined with increasing litter size.

We characterized circumstances associated with each litter move for both species to help elucidate potential underlying causes. Predation was denoted as a potential causal factor when predator activity occurred within close proximity to the natal burrow at the time of the move. Trapping disturbance was denoted when the litter was moved in immediate association with trapping efforts. Habitat was indicated when the move resulted in improved habitat quality, based on long-term data on occupancy and reproductive success throughout both study areas. We also summarized conspecific interactions associated with litter moves to explore the potential role of the social environment. Female relatedness was calculated from pedigrees based on mother–pup and littermate relations (Armitage & Johns, 1982; Wells et al., 2017).

3 | RESULTS

The method of transporting pups was similar for both species (Figure 1). One pup was transported at a time. Mothers often paused in transit and released the pup, presumably to rest or scan for predators, then grasped the pup and continued, allowing identification of how the pup was grasped. The mother nuzzled the pup's underside, prompting it to curl up into a ball on its back with at least some feet apparently clasped together. The mother seized the pup in the area of its feet and belly with her incisors; in many cases, she appeared to secure the clasped feet of the pup in the diastema between her incisors and premolars, and in other cases, she might have seized the skin and fur of the belly in her incisors. Moving a litter was a continuous process until the entire litter was relocated, and aside from pauses while in transit, we did not observe delays by the mother in moving portions of a litter.

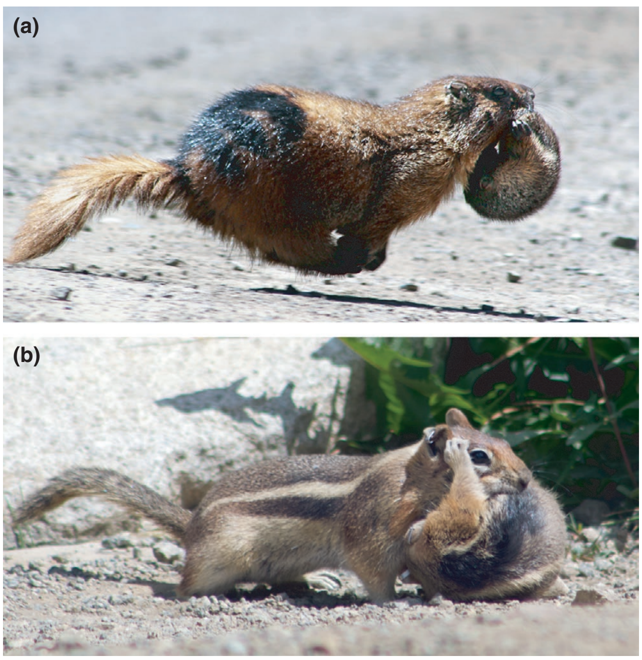

FIGURE 1 Litter relocation behavior by a yellow-bellied marmot (a) and golden-mantled ground squirrel (b), in which the mother seizes the pup in the area of the feet and belly with their incisors and carries it upside–down

We observed a total of 32 litters relocated by 24 GMGS mothers and 19 litters relocated by 17 YBM mothers; six GMGS and two YBM moved their litters during more than 1 year. Mothers that moved litters ranged in age from 1 to 7 years for GMGS and 2 to 10 years for YBM, age ranges that are similar to the reproductive life spans for each species (Armitage, 2014; Moore, Wells, Van Vuren, & Oli, 2016). Excluding two YBM relocations that originated outside our four study colonies, the frequency of litter relocation for GMGS (0.21, $n = 153$ litters produced) was about twice as great as that for YBM (0.10, $n = 172$ litters produced). Furthermore, eight GMGS litters were relocated multiple times in sequence, with up to five relocations for one litter, for a total of 44 GMGS relocation events. We did not observe multiple relocations of YBM litters.

We were able to measure the distance that females moved their litters in all 19 YBM relocation events and in 40 GMGS relocation events; four GMGS relocation events were excluded because one of the two endpoints was uncertain. Of the 19 YBM litter relocations, 16 were internal moves and three were external moves (from one colony to another, from a solitary site to a colony, or from one solitary site to another). Of the 40 GMGS litter relocations, 36 were internal moves, and four were external moves. Thus, 16% of YBM relocation events and 10% of GMGS relocation events involved movement outside the normal spatial context of the mother. The mean size (± *SE*) of relocated litters was 4.2 ± 0.3 YBM pups and 4.8 ± 0.3 GMGS pups. Spearman's rank correlation coefficients did not show a significant correlation between litter size and relocation distance for either YBM ($r_s = -0.317$, $p = .19$, $n = 17$) or GMGS ($r_s = 0.001$, $p = 1.00$, $n = 23$).

A Mann–Whitney U test did not reveal a significant difference between GMGS ($n = 23$) and YBM ($n = 17$) in the distance that mothers moved their litters during relocation events (U = 239.5, $p = .23$; Table 1). The same outcome resulted when considering internal moves only (GMGS, $n = 19$; YBM, $n = 14$; U = 182.5, $p = .07$), and also when considering external moves (YBM, $n = 3$; GMGS, $n = 4$; U = 1, $p = .11$). The total distance traveled by the mother when relocating a litter was substantial in some cases, approaching a maximum of 3 km for both species (Table 1).

We identified general similarities between YBM and GMGS in potential causes associated with litter relocations. In both species, litter relocation was often associated with disturbance due to trapping (five YBM relocations and 17 GMGS relocations) or an improvement in habitat quality (six YBM and five GMGS). For example, in two cases for GMGS a female moved her litter during a trapping event, then moved the litter back to its original location within 24 hr of traps being removed. In almost all relocation events, a mother remained with her litter at the new location. However, we observed two instances in

TABLE 1 Summary of distances that golden-mantled ground squirrels (GMGS) and yellow-bellied marmots (YBM) moved their pups

	GMGS			YBM		
	Mean	Median	Range	Mean	Median	Range
Relocation distance (m)	94 ± 13	79	16–252	85 ± 23	46	15–324
Internal move distance (m)	71 ± 10	56	16–160	43 ± 5	46	15–73
External move distance (m)	203 ± 16	189	182–252	279 ± 33	298	216–324
Total distance moved (m)	791 ± 153	462	94–2,802	598 ± 181	315	100–2,682

Note: Mean values are reported ± *SE*.
Total distances were calculated by multiplying the relocation distance by the number of trips each adult female would have to take to move her entire litter (number of pups in litter, multiplied by two, minus one).

which a female GMGS moved her litter to a location outside of her home range and then returned to her original location alone (hereafter called “litter dumping”); both of these external moves, plus a third move that originated outside of the study area, involved moving and then abandoning pups at locations known to be of high-quality habitat. The first two moves occurred on the day the litter emerged from the natal burrow, the third occurred on that day or shortly thereafter, and in all three cases the litters were female-biased, averaging 83% female pups. Predation (one YBM, seven GMGS) potentially influenced both species to relocate litters; for YBM the predator was coyotes, and for GMGS the predators were red foxes and weasels. The social environment also may have played a role. YBM moved litters away from aggressive females, presumably to avoid social conflict (n = 3), or toward neighboring female relatives, presumably to benefit from proximity to kin (n = 2). Although interactions among adult GMGS were mostly agonistic, we observed three cases in which GMGS females moved their litters closer to related females, sometimes despite relocating to an area of greater local density (and thus presumably greater competition for resources). We could identify no potential causal factors for two YBM and 15 GMGS litter moves.

4 | DISCUSSION

Our observations provide the first photographic documentation and distance calculations for litter relocation behavior in YBM and GMGS. Given positive relationships between space use and body size in mammals (Jetz et al., 2004), we were surprised to find that litter relocation distance for internal moves was not greater for the large-bodied YBM than for the small-bodied GMGS. The explanation may lie in space-use behavior of the two species. Home range size for adult female GMGS averages 1.85 ha (100% minimum convex polygon, n = 44; Aliperti, unpublished data), more than twice the average size of home ranges for adult female YBM at the colonies we studied (0.77 ha, 100% minimum convex polygon, n = 11; calculated from Armitage, 2009, Figure 1). Home range size for YBM is smaller than that of any other marmot species, and smaller than that expected based on body mass; this small size is likely influenced by the high concentration of food resources in YBM home ranges (Armitage, 2009, 2014). Hence, it is possible that internal relocations by YBM were not greater than GMGS in distance because spatial contexts of the two species did not differ accordingly. Not surprisingly, mean distances for each species for internal relocations were less in magnitude than the diameters of the average home range for GMGS (153 m) and YBM (99 m; diameters were calculated considering the home range as a circle). Female GMGS relocated their litters more frequently than YBM, for uncertain reasons. Perhaps the small-bodied GMGS is more vulnerable to predation than YBM, thereby providing a greater motivation for litter relocation. Also, differing social constraints may have had an influence. GMGS are considered to be solitary and territorial (Michener, 1983); hence, a female might relocate her pups anywhere within her home range without encountering neighboring females. In a YBM colony, however, females share space with other females in the matriline (Armitage, 1991); thus, the presence of multiple adult females within a home range, including some females that might be behaviorally dominant (Armitage, 1991), may restrict litter relocation opportunities.

A female presumably decides to relocate her litter when the benefits of doing so exceed the costs (Clutton-Brock, 1991; Gross, 2005). Possible costs include increased exposure to predation and energy expenditure. We observed no predation events during litter relocations, but the energy expenditure can be substantial; the longest relocation distances we observed represent 4.6 and 2.5 times the expected daily movement distances for female GMGS and YBM, respectively (Garland, 1983). If energetic cost influenced the decision to relocate a litter, then we expected that females either would be more likely to relocate small litters, or would relocate small litters farther distances. In both species, however, the size of relocated litters was not smaller than that of the long-term average litter size for the populations we studied, and there was no correlation between litter size and relocation distance.

We observed several possible benefits of litter relocations. For both GMGS and YBM, many relocations were associated with trapping or the presence of predators; in both circumstances, the motivation of the mother might be to reduce the perceived threat to her pups. Habitat quality and kinship also potentially influenced litter relocations in both species. All three cases of litter dumping involved GMGS relocating weaned litters with female-biased sex ratios to high-quality habitat; the long-term sex ratio for the population is 51% female pups (Wells & Van Vuren, 2017). Females are the philopatric sex in our population of GMGS. Thus, litter dumping may represent a form of parental investment opposite to bequeathal (Harris & Murie, 1984); instead of a female leaving her high-quality burrow to her daughters, she may move her daughters to a high-quality location and leave them. To our knowledge, no other cases of litter dumping have been reported for ground-dwelling squirrels. Given the importance of kin to social structure in YBM (Armitage, 2014), it is not surprising that this species sometimes relocated litters closer to kin. Although female GMGS are considered asocial (Michener, 1983), female philopatry results in the formation of kin neighborhoods (Wells & Van Vuren, 2017); hence, kinship might play a role in litter relocation. Future studies should continue to explore litter relocations to better understand the ecological causes and consequences of this behavior.

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CONFLICT OF INTEREST

The authors declare that they have no conflict of interest.

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