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ARTICLE

Alloparenting in Steller sea lions (*Eumetopias jubatus*): correlations with misdirected care and other observations

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Abstract Alloparental care is rarely observed in Steller sea lions (*Eumetopias jubatus*) where maternal care is extended to a single pup for up to 1 year or more. However, we observed 28 allonursing events and one case of adoption at a small breeding rookery in the western Gulf of Alaska between the years 2001 and 2005. Multiparous and primiparous females were observed nursing nonfilial individuals with equal frequency, but primiparous females spent significantly more time nursing nonfilial individuals. Multiparous females allowed allonursing only while sleeping and unaware while most primiparous females were aware that they were allonursing. These results are consistent with the misdirected-care hypothesis suggesting that primiparous (presumably younger) females nurse nonfilial pups due to inexperience, whereas multiparous (presumably older) females are victims of milk stealing during times of inattentiveness. Nonfilial pups were aggressively tossed most often during the pupping season and only by multiparous females, while allonursing events occurred more frequently after the pupping season. Starveling pups were not cared for by any female, but two were attended by a single bull during separate autumn seasons.

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Introduction

Alloparental care, when an individual provides nourishment, protection, or other forms of care to nonfilial offspring, can be energetically costly, and based on natural selection arguments, should be maladaptive. The reasons for such care, although poorly understood, may result from misdirection, the need to acquire maternal experience, necessitation of milk evacuation, a high degree of kinship (Packer et al. 1992; Riedman 1982; Roulin 2002), suppression of kin recognition during lactation (Roulin and Hager 2003), and/or the need to maintain hormonal balances (Roulin 2003). Pups may also seek out alloparental care for additional nutrition (Packer et al. 1992) and/or for immunological benefits (Roulin and Heeb 1999). Alloparenting has been documented in a wide variety of birds and mammals, although the extent to which it occurs can vary dramatically among species (e.g., Pusey and Packer 1994) and within a species (e.g., Boness et al. 1992) depending upon litter size, degree of crowding, weather conditions, scarcity of resources or levels of aggression (Packer et al. 1992; Riedman and Le Boeuf 1982; Roulin 2002). Therefore, we may be able to test specific hypotheses about the occurrence of alloparenting by examining the social structure and natural environment in various groups of animals.

Among pinnipeds, different forms of alloparental care such as adoption and allonursing have been reported in several phocid species and less commonly in

otariids (Boness et al. 1992, 1998; Lunn 1992; Riedman 1982; Riedman and LeBoeuf 1982; Stirling 1975). In the Steller sea lion (*Eumetopias jubatus*), an otariid that gives birth to one pup per year and extends maternal care for up to 1 year or more (Pitcher and Calkins 1981), nonfilial offspring are rarely tolerated and are at risk of obtaining injuries by being tossed or bitten (Sandegren 1970). In this well-studied species, alloparental care has been observed very infrequently in the form of allonursing (Higgins 1984; Porter and Trites 2004), adoption (Riedman 1982, Table 1), and guarding/protection by a male (Sandegren 1970, p. 75). Allonursing may include any temporary or indiscriminate nursing between a female and nonfilial pup; whereas adoption implies exclusive care of a foster pup including nursing, protection, and perhaps training of nonfilial offspring over longer time periods (Riedman 1982).

We report several observations of alloparental care observed at a small Steller sea lion rookery in the Northern Gulf of Alaska and examine correlations with maternal experience and levels of aggression. We may predict that females who nurse alien offspring alongside their own, whether primiparous (having produced her first offspring) or multiparous (given birth more than once), would not have the need to gain parenting experience because nursing their own pup should be sufficient (Roulin 2002). We may also predict that females who allonurse only when they are unaware of it and reject nonfilial pups upon discovery are probably victims of milk theft, which is consistent with the hypothesis of misdirected care (Packer et al. 1992). Furthermore, misdirected care may also be implicated in cases where primiparous females are more tolerant of allosuckling pups compared to multiparous females. The foregoing predictions do not necessarily preclude other hypotheses such as kin selection, reciprocity, etc., and those alternatives are discussed. Although our sample sizes were small, the data presented here should assist in our understanding of the causes and function of alloparenting in Steller sea lions and other pinnipeds.

Study area

This study was conducted over the years 2001–2005 at a Steller sea lion rookery on Chiswell Island (59° 36.13′N, 149° 34.05′W), located in the northern Gulf of Alaska and part of the U.S. Fish and Wildlife Service Alaska Maritime National Wildlife Refuge. The rookery consisted of about 90 breeding animals producing up to 80 pups per year and was generally occupied from late May through October (Maniscalco et al. 2006). Observations of the sea lions were accomplished using a remote control video system installed on the island by SeeMore Wildlife Systems, Homer, Alaska, at the request of the Alaska SeaLife Center. The video system consisted of six cameras placed at intervals along the length of and above the rookery for a complete view of the animals from different directions. Cameras were operated and viewed in real time at the Alaska SeaLife Center 65 km to the north in Seward, Alaska. See Maniscalco et al. (2006) for more details on Chiswell Island and the remote video system.

Materials and methods

Data concerning alloparental care and aggression (specifically pup tossing) were collected opportunistically in conjunction with ongoing remote video studies of maternal care, which included knowledge of the parity of many female sea lions (Maniscalco et al. 2006). All sea lions with distinguishable scars, fungal patches, or other unique markings were watched closely from their first arrival on shore every year. Summer observations were conducted from at least 06:00 to 22:00 daily. Additional morning and nighttime observation hours were added as light levels allowed. After 10 August, observations were made from approximately sunrise to sunset as daylight diminished into the autumn season. We conducted scan samples for all identifiable females and their pups during even hours of the day and full census counts of all sea lions at 11:00 and 19:00 from late May through August and at 11:00 through the rest of the year.

An allonursing event was considered to occur when an individual was observed nursing two pups simultaneously; suckling a pup or yearling that was confirmed as nonfilial from research tags, brands, or natural markings or by the reproductive history of the nonfilial mother; nursing two yearlings simultaneously; or when an adult animal was observed suckling. If there was any doubt that a female was not related to the allosuckler, the event was not included in the analysis (four cases). Most aggressive encounters and allosuckling events were videotaped for later analysis, while others were only noted with a database entry and/or a digital picture or video clip.

We used Observer Pro 3.0 software (Noldus Information Technology, Leesburg, VA, USA) to analyze videotapes of allonursing events to determine total onteat duration of nonfilial and filial individuals and total number of vocals from females toward nonfilial

individuals. To assess temporal changes in allomaternal care and aggression, we divided our observation period into three seasons: the pupping season (25 May–05 July), post-pupping summer (06 July–18 August) and autumn (19 August–30 October) following Maniscalco et al. (2006). Behavioral comparisons between multiparous and primiparous females were conducted using SigmaStat 2.03 (SPSS, San Rafael, CA, USA). Additional observations of alloparental care were summarized descriptively.

Results

We conducted 11,200 h of observations on 782 days between 25 May and 30 October over the years 2001–2005. There were an average of 43 pups and yearlings on the rookery during that period. We observed 28 allonursing events between females and nonfilial pups, juveniles, and adults during those years; however, allonursing was most commonly observed in 2004 (17 occurrences) when pup numbers were greatest (Maniscalco et al. 2006). There were also 17 occurrences distributed through all years of the study that included simultaneous nursing of the filial pup. One allonursing event observed in 2003 and one in 2004 included more than one nonfilial individual suckling a single female simultaneously. The latter of those also included the filial pup, such that three individuals were simultaneously suckling one female. We could not determine the extent that same individual pups were attempting to allosuckle but suspect this probably occurred a few times in 2004. The sex of the allosuckling pup was known in only two cases; one male, one female.

Allonursing was observed only twice during the pupping season and more commonly occurred after 5 July (Fig. 1). For individuals whose parity was known, primiparous females nursed nonfilial offspring longer (median=359.1 s, n=8) than multiparous females (median=29.8 s, n=8; Mann–Whitney rank sum, P=0.028). Unless they were sleeping, multiparous females would not allow nonfilial pups to suckle and would immediately terminate any allosuckling as soon as they became aware of the nonfilial individual; whereas, seven of eight primiparous females allowed allonursing to continue even when aware of it.

There was a tendency for primiparous females to vocalize aggressively toward nonfilial individuals less frequently (median=0.10 vocals/min) than multiparous females (median=0.65 vocals/min) during allonursing, but the difference was not significant (Mann–Whitney rank sum, P=0.442), possibly because of the small sample size. Females were never observed to toss allosucklers, and biting was rarely observed. However, 19 pups were observed to be aggressively tossed for other reasons during the 5 years of this study (Fig. 1). All but two of those instances occurred during the pupping period, and when their status was determined (n=8; 11 tosses), all tossing females were multiparous.

We witnessed one case of adoption during our study period with a female that had given birth every year since at least 2000. In 2003, she gave birth to a live pup on 03 June that was later confirmed dead through video observations on three occasions between 11 June and 18 June. On 20 June, she was observed nursing another pup and exhibiting behaviors typical between mom and pup pairs such as maternal attentiveness and nuzzling. The sexes of the dead pup and the adopted pup were not determined. Between 20 June and 01

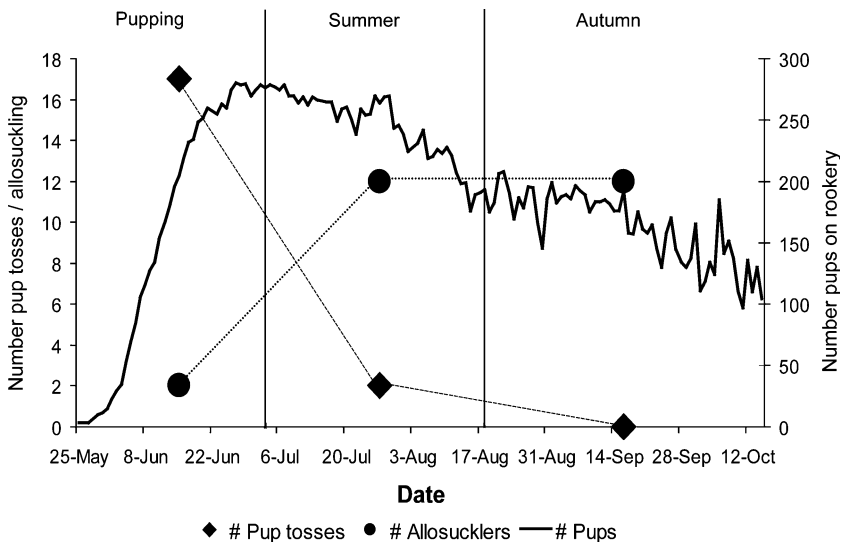

Fig. 1 Total number of pups on the rookery, number of pups tossed and allosuckling events observed during different seasons for years 2001 through 2005 combined. Seasons were divided into pupping (25 May–05 July), summer (06 July–18 August), and autumn (19 August–31 October). The number of pups (*z-axis*) is displayed to represent the size of the rookery through the seasons and should not be used to gauge the relative occurrence of allosuckling without taking into account the hours of observation

December, the adopting female was seen with her foster pup a total of 582 times and observed nursing it on 50 of those occasions. The identity of the adopted pup's biological mother was not known but was probably one of several females that were not tracked because they lacked reliable natural markings. The adopted pup was not observed to suckle from any other female except its foster mother as of 20 June. The foster mother returned to the rookery the following summer to give birth again and was never observed in the years prior or subsequent to 2003 to allonurse or provide any maternal care to a pup other than her own. It was also noted that during this study period, at least 19 other pups died or were lost to high surf conditions during the month of June, but none of their mothers were observed to adopt another pup.

On three occasions during the summer season, pups were abandoned by their mothers. Those pups subsequently starved and died and were not attended by any adult sea lion. However, two abandoned and starveling pups during the autumn seasons of 2002 and 2003 were attended by one individual bull at Chiswell Island. In 2002, the starveling, which had a unique brand originating from Sugarloaf Island, 170 km west of Chiswell, was observed spending a total of 6.5 h with the bull during a 2-day period. On the second day, after neither was present for nearly 24 h, they were observed hauling out together on Chiswell Island. The pup often lay side by side with the bull and made 121 suckling attempts during 10 ersatz suckling bouts. Suckling by the starving pup was directed toward the ventral side of the bull in the approximate area of teats, although teats were not visible. The longest ''suckling bout'' observed was 73 min and the shortest was 3 min. Suckling was only observed with this particular bull, although the pup also spent 1.2 and 0.7 h with two other bulls. In 2003, the same bull was observed spending a total of 14.2 h with a different, unmarked starveling pup during a period of 2 days compared to 2.0 h spent with one other bull. That pup made 293 suckling attempts during three ersatz suckling bouts (range 5–74 min). Both pups were presumed to have eventually died. The pup in 2003 was actually observed to fall into the water and was unable to haul out again.

Discussion

Allosuckling is a very rare event among Steller sea lions (Porter and Trites 2004) and our data should not suggest otherwise even though we observed its occurrence at a site with relatively few pups (≤80; Maniscalco et al. 2006) compared to other studies of this species (Milette and Trites 2003 [≤2,575 pups], Porter and Trites 2004 [≤266 pups]). It is likely that we were able to witness this unusual behavior several times because of many thousands of hours of observation. It is also possible that we witnessed this behavior comparatively often because there may have been a higher proportion of younger females at Chiswell Island than other rookeries studied (Higgins 1984; Milette and Trites 2003). Additionally, we may have observed allonursing more frequently than Porter and Trites (2004) because their observations were conducted during winter and spring when milk would have been a more costly resource. Females have the increased energetic demands of a growing fetus in those seasons (Pitcher et al. 1998), and therefore, could be less tolerant of milk theft.

Regardless of overall frequency, multiparous (presumably older) females at Chiswell Island nursed nonfilial offspring just as often as primiparous females, but the latter allowed allosuckling for much longer periods. Longer suckling bouts, together with the tendency for primiparous females to vocalize aggressively to nonfilial offspring less often than multiparous females, indicate that younger females may be naïve to the energetic costs associated with allosuckling or have limited ability to recognize their own offspring; whereas, older females are primarily victims of milk stealing. These observations are consistent with the misdirected maternal care hypothesis outlined by Roulin (2002) but are not likely due to the need to gain maternal experience because primiparous females allowed nonfilial pups to nurse alongside their own. Nursing their own offspring should be sufficient for new mothers to gain experience (Roulin 2002). We emphasize here that the apparent inexperience of primiparous females observed in this study is considered a subcategory of the misdirected care hypothesis (Roulin 2002) and should not be confused with the hypothesis which suggests that young females may allonurse to gain maternal experience (Riedman 1982).

Our assumption of maternal error to explain allonursing in Steller sea lions does not necessarily exclude the possibility that some other factors may also play a role in the occurrence of this behavior. Allonursing, although rare, may be a more regular occurrence at Chiswell Island than at larger rookeries and haulouts where it was scarcely observed (Higgins 1984; Milette and Trites 2003; Porter and Trites 2004) because closely related individuals may be encountered more readily in small animal groups (Murray 1985) and Steller sea lions have a propensity to return to, and pup at, their natal rookery (Raum-Suryan et al. 2002). Therefore, the hypothesis relating close kinship to

alloparental care cannot be ruled out. Reciprocity is also more likely to occur in small groups (Boyd and Richerson 1988). We were unable to determine if females nursed each other's offspring equally but feel that it was unlikely because a few females allonursed much more than most others.

We could not test the hypothesis that allonursing females needed to evacuate additional milk because we made no measure of lactation in these animals. If primiparous females produced more milk than multiparous females, our data would lend some support to that hypothesis. However, milk production is positively correlated with mass in pinnipeds (Arnould and Boyd 1995; Iverson et al. 1993; Mellish et al. 1999), and female Steller sea lions continue to gain mass for several years after the age of first reproduction (Winship et al. 2001). This suggests that older, multiparous females produce more milk than younger, primiparous females. Therefore, primiparous females may have less need to expel excess milk than multiparous females, making this hypothesis unlikely.

It has also been proposed that some communally breeding species nurse alien offspring due to genetic suppression of kin recognition that benefits the offspring of polygynous males by allowing their progeny access to milk from several females (Roulin and Hager 2003). That hypothesis is also doubtful in the case of Steller sea lions because the females may move around to different areas of the rookery between the time they breed and subsequent pupping a year later (Parker 2006). Therefore, pups with the same father do not necessarily stay in the same territory and furthermore, pups disperse throughout the rookery by mid-July (ASLC, unpublished data) making it likely that allonursing females would suckle offspring of different males.

We rarely observed allosuckling during the pupping season, the time when pups were tossed most often. Aggressive pup tossing during pupping could relate to the pups being lighter and easier to pick up compared to later in the season, or it may occur because females are more aggressive during June due to drastic hormonal changes that occur between parturition and estrus (Atkinson 1997), or because there is a greater need for protection of their own newborns. Similary, South American fur seal (*Arctocephalus australis*) females become very aggressive just after pupping (Harcourt 1991). Therefore, pups may be deterred from allosuckling or milk stealing when they are very young due to greater risk of injury from nonfilial mothers. Steller sea lion pups also become increasingly active and exploratory after 4 weeks of age (Gentry 1974; ASLC, unpublished data) when they would more frequently encounter other females that may be agreeable or oblivious to allosuckling.

It is interesting to note that only multiparous females were observed to aggressively toss nonfilial pups. Female aggression toward nonfilial offspring is commonly observed in otariids (e.g. Harcourt 1991; Trillmich 1981), but no correlations with maternal age or experience have previously been reported. It is possible that some first-time mothers do not have a well-developed ability to identify their own pups and therefore are more tolerant of nonfilial pups. There are still many gaps in the study of kin recognition among pinnipeds, although it is generally accepted that vocal recognition is more strongly developed in otariids than phocids (Insley et al. 2003). It would be disadvantageous for a female to toss or bite her own pup because she did not recognize it, so leniency would be adaptively preferential in regards to aggression toward pups until offspring recognition is well learned. These observations of the lack of aggression toward nonfilial pups provide additional evidence that primiparous Steller sea lions may lack maternal experience, which could result in misdirected care.

We did not observe starveling pups suckling nonfilial females, although Porter and Trites (2004) reported a starveling Steller sea lion pup sneak-suckling and being rejected when discovered. Starvelings may be more likely rejected than well-fed pups because they could be recognized as being too costly to provide sufficient nourishment for regaining health or because they vocalize more and are less stealthy in attempts to steal milk. Yet, one particular bull attended to two different starvelings during subsequent autumn seasons. That behavior might be considered allopaternal care since it is extremely unlikely that this bull sired those pups, one of which came from a different rookery. It is equivocal if such behavior could be considered truly alloparental since he could not have provided nourishment in the form of milk. However, he tolerated the pups' behavior more than any other male or female sea lion, probably provided warmth to the starvelings by physical contact, and may have been accompanied by one of them while foraging as they were seen hauling out together after being away from the rookery for 24 h. Smith (1968) observed starving or weak grey seals attempting to suckle on seaweed, boots of observers, each other, and bulls indicating that this is probably an inherent behavior used in the search for nourishment. Possible alloparental care by a young bull toward a newborn pup and similar suckling behavior by the pup was also observed at another Steller sea lion rookery in 1968 (Sandegren 1970, p. 75), but this type of behavior is probably extremely rare in otariids.

The single case of adoption that we observed is also very unusual in otariids and not consistent with misdirection or the need for gaining maternal experience since the foster mother was known to have successfully raised young in the previous 3 years and never was otherwise known to have permitted nonfilial offspring to suckle. This adoption may be more suggestive of the need for neuroendocrine regulation of hormones (Roulin 2003) or the need to express milk, although we have no data to support this and therefore other hypotheses should not be excluded. Roulin (2003) argues that suckling behavior promotes production of the hormone prolactin through teat stimulation, which is known to enhance immune response, improve maternally derived immunity to neonates, and allow a female to adjust the timing of her next pregnancy. Riedman and Le Boeuf (1982) also suggested that fostering may be a means of maintaining reproductive cycles. Further evidence of this is implicated by the observation that females who did not pup or lost their pup at Chiswell Island were less likely to pup the following season than females who did not lose their pup (ASLC, unpublished data). The adopting female in this study gave birth in the following season, which does not refute this assumption. However, we cannot rule out the need to evacuate milk (Roulin 2002; Wilkinson 1992) as a possible reason for adoption in this case or simply an inherent desire to care for conspecific young (Alcock 1989).

The hypotheses put forward to explain the occurrence of allosuckling and other forms of alloparental care are probably not mutually exclusive (Roulin 2002), and factors affecting them can vary among species within the mammalian class (Riedman 1982). For instance, density of animals appears to be positively correlated with the occurrence of allosuckling and fostering in phocids (Boness et al. 1998; Riedman and Le Bouef 1982) but may be negatively correlated with density in fur seals (Lunn 1992) and possibly Steller sea lions because of the few occurrences of this behavior at large rookeries and haulouts (Higgins 1984; Porter and Trites 2004) compared to the several occurrences at the small rookery we studied at Chiswell Island.

The reasons for alloparental care may also vary within a species depending on how the care is expressed. The data and discussion presented in this paper strongly suggest that allonursing in Steller sea lions and perhaps other otariids (Lunn 1992) results from two types of misdirected care: (1) milk stealing when females are unaware of nonfilial suckling and (2) maternal inexperience if young, primiparous females lack the ability to distinguish there own pup. In contrast, the one case of adoption observed in this study was even more unusual and may be attributed to other factors not examined. Overall, this study should provide a better understanding of the proximate factors that affect the occurrence of alloparental care in Steller sea lions and may apply to some other species.

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