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Primiparous females do not exhibit reduced maternal care in gray seals (*Halichoerus grypus*)

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Abstract

We compared the behaviors of primiparous and multiparous gray seal (*Halichoerus grypus*) females over the course of lactation to examine whether poorly developed maternal behaviors may play a role in the reduced lactation performance observed in primiparous females. Overall, primiparous females spent as much time interacting with their pups as multiparous females. The proportion of time spent nursing their pup increased significantly between early and peak lactation in both primiparous and multiparous females. Although there was no significant difference in the duration of nursing bouts as a function of reproductive status, primiparous females nursed significantly more frequently (bouts/hour) and, therefore, spent a significantly greater proportion of time nursing than multiparous females throughout lactation. Primiparous gray seal females were also significantly more active than multiparous females, however, the difference in activity represented only a small proportion of the overall time budget. We conclude that poorly developed maternal

behaviors resulting from a lack of prior reproductive experience are unlikely to account for lower levels of milk energy transfer to pups in primiparous gray seals.

Key words: gray seal, *Halichoerus grypus*, lactation, maternal behavior, milk energy transfer, nursing, primiparous, reproductive experience.

The most significant determinant of offspring growth during lactation is the ability of females to transfer milk energy to their neonates. Lactation is the most energetically expensive period in the life of a female mammal (Gittleman and Thompson 1988) and females offset these costs by increasing energy intake and/or mobilizing body energy stores. Because females of many species typically begin to reproduce before reaching full adult body size, lower neonatal growth rates and weaning masses in novice breeders are often assumed to result from limits on the energy available for milk production as a consequence of smaller absolute levels of body energy stores and/or a smaller gut capacity. However, while increases in body mass in young females often correlate with improved lactation performance (*e.g.*, Derocher and Stirling 1994, Weladji *et al.* 2002, Broussard *et al.* 2003, Bowen *et al.* 2006), energy availability may not be the only factor. The transfer of milk energy to offspring by primiparous females may also be reduced relative to multiparous females as a consequence of lower levels of maternal care. Studies in both laboratory and domestic species demonstrate that cycles of pregnancy, parturition, and lactation (reproductive experience) play a direct role in the development of maternal behaviors through a series of complex changes that occur within the brain. Although the specific hormonal cues appear to differ among species, changes in synaptic structure as well as neurotransmitter and receptor functions are initiated during a female's first reproductive effort by the hormones associated with pregnancy, parturition, and the onset of lactation. These neurological changes are reinforced by the subsequent interactions with offspring and are then carried over into the next reproductive cycle. As a result, in some species multiparous females show significant improvements in both the intensity and quality of maternal behaviors compared to primiparous females (see Dwyer and Lawrence 2000, Fleming and Li 2002, Gonzalez-Mariscal and Poindron 2002, Kinsley *et al.* 2006, Numan *et al.* 2006 for comprehensive reviews). To date, studies examining the influence of prior reproductive experience on maternal care in free-ranging mammals have been limited to comparisons of abandonment rates or observations of allonursing (Reiter *et al.* 1981, Maniscalco *et al.* 2007). Thus, whether cycles of pregnancy, parturition, and lactation may have a significant influence on the development of maternal behaviors related to the transfer of milk energy to offspring in natural populations remains poorly studied.

Gray seals (*Halichoerus grypus*) are colonial breeders. On Sable Island (Nova Scotia, Canada), females come ashore between December and February to give birth on the sand beaches surrounding the island and on the vegetated and nonvegetated dunes that extend along its length. Females give birth to a single pup, there is no allomaternal or paternal support and pups consume only milk during the lactation period. Females and their pups are typically found in loosely defined clusters with adult males maintaining positions near females and competing for the opportunity to mate (Boness and James 1979). Lactation is brief (16–18 d, Bowen *et al.* 1992) and copulation occurs on land 2–3 d prior to weaning. In contrast to species like the northern elephant seal (*Mirounga angustirostris*), in which females compete for favorable positions within harems (Reiter *et al.* 1981), there are no dominance

interactions or competition for parturition sites among gray seal females (Boness and James 1979). At the end of lactation, females abruptly wean their pups and depart the breeding colony. Pups then rely on the energy stores acquired during the lactation period to survive a postweaning fast and the transition to nutritional independence (Noren *et al.* 2008). The total milk energy intake of pups is the strongest predictor of pup weaning mass and condition in gray seals (Mellish *et al.* 1999). In turn, weaning mass and condition presumably affect postweaning survival, as reported in another population, with larger, fatter pups having a greater probability of surviving to 1 yr of age (Hall *et al.* 2001, 2002). Therefore, the ability of females to rapidly transfer milk energy to their offspring is a critical determinant of maternal reproductive success in gray seals.

Like most other large-bodied phocid seals (Family Phocidae), gray seals are capital breeders (Boness and Bowen 1996). On Sable Island females remain ashore with their pups throughout the lactation period, relying entirely on the body energy reserves acquired prior to parturition to support both the energetic costs of milk production and their own metabolic overhead (Iverson *et al.* 1993). Primiparous gray seal females wean significantly lighter pups (Bowen *et al.* 2006). Because gray seal females begin to reproduce at 4–6 yr of age, well before reaching full adult body size in their early to middle teens (Bowen *et al.* 2006, 2007), this reduced lactation performance has been attributed to their smaller absolute levels of body energy stores alone (Bowen *et al.* 2006). However, poorly developed maternal behaviors in primiparous females could also have a significant influence on the transfer of milk energy to pups either directly, through reduced time spent engaged in nursing behavior, or indirectly, through higher levels of activity. As a capital breeder, the energy available to support both milk production and maternal maintenance in gray seals is limited by the level of body energy stores at parturition. Female gray seals spend the majority of their time resting during lactation (Boness and James 1979), which can be an effective mechanism for reducing the proportion of total body energy reserves expended on maintenance metabolism and, thus, maximizing the energy available for milk production (Gittleman and Thompson 1988). If, as has been observed in laboratory species (Wartella *et al.* 2003), primiparous females show a greater sensitivity to disturbance during lactation this could result in an overall greater level of activity and, thus, a reduction in the energy available for milk production. We compared the behaviors of primiparous and multiparous gray seal females over the course of lactation to test the hypothesis that poorly developed maternal behaviors contribute to the reduced lactation performance observed in primiparous gray seal females. We predicted that primiparous gray seal females would spend less time interacting with their pups and, in particular, less time engaged in nursing behavior than multiparous females. We also predicted that primiparous females would show higher levels of activity throughout lactation.

Materials and Methods

Our study was conducted on Sable Island (43°55′N, 60°00′W), located approximately 300 km ESE of Halifax, Nova Scotia, Canada during the 2004 through 2006 breeding seasons. Females in this population begin reproducing at 4–6 yr of age and can continue to reproduce to age 30 or more (Bowen *et al.* 2006, 2007). The study females were a subset of those that were permanently marked as pups between 1985 and 1989 and between 1998 and 2002 with unique, hot-iron brands

shortly after weaning and, thus, were of known age. As with other gray seal colonies (Allen *et al.* 1995, Pomeroy *et al.* 2000), the Sable Island gray seals exhibit a strong philopatry with an estimated fidelity rate of 98.4% (W. D. Bowen, unpublished data). Weekly whole-island censuses of all branded individuals combined with daily surveys throughout the colony during the breeding season have been conducted in this population since 1983 (see Bowen *et al.* 2006 for details) and, thus, the reproductive histories of all females in the study were known. The multiparous females ($n = 8$) in our study were 18–21 yr of age and had been observed pregnant and/or rearing a pup in a minimum of 10 previous breeding seasons. The primiparous females ($n = 8$) we studied were 4–6 yr of age. Females were considered primiparous if they had not been observed pregnant or rearing a pup in a previous breeding season. Given the frequency of whole island censuses and colony surveys, it is highly unlikely that a female returning to the colony to give birth would not have been detected. Nonpregnant females are rarely observed among lactating females on Sable Island. Of the 311 females from the 1998 to 2002 cohorts, which recruited to Sable Island, none were sighted on Sable Island or at any other colony in breeding seasons prior to the first year they were observed with a pup. Therefore, we are confident that the first year a female was observed with a pup, she was primiparous. While the number of females giving birth on Sable Island has increased dramatically since the mid 1970s (Bowen *et al.* 2003) with an estimated 41,500 pups born in 2004 (Bowen *et al.* 2007), during the years of the study there was still unoccupied breeding habitat and areas with low densities of breeding females (Bowen *et al.* 2006). Therefore, in contrast to observations for some other phocid seals (*e.g.*, Reiter *et al.* 1981), there is no evidence that females returning to the colony to breed for the first time are marginalized into areas of higher density or poorer breeding habitat. All females had known parturition dates and both females and pups were marked with a water-soluble dye on the day of parturition to aid in identification.

To standardize the level of interaction with conspecifics as much as possible, observations were conducted in areas of low-to-moderate density, where density was estimated by counting the number of adults within 10 m of the focal females. The behaviors of females and their pups were recorded by video camera once during early lactation (day 2–6 postpartum) and again at peak lactation (day 9–13 postpartum, Iverson *et al.* 1993) for a total of 32 observation periods. For each pair, the two recordings were separated by a minimum of 6 d. Pairs were videotaped (Hi-8 format) from 0900 to 1600, using Fieldcam video systems (Furham Diversified Inc., Seabrook, TX), which ran automatically throughout the observation period powered by a 12 V marine battery. Cameras were placed on the dunes overlooking pairs to allow camera setup without disturbance of the animals. Females were identified on video by their brand and/or dye mark. Tapes were transcribed using The Observer software (Version 4.0, Noldus Information Technology, Wageningen, Netherlands) to score behaviors while watching the tapes on a large video monitor. Durations of recorded behaviors were converted to percentage of total observation time.

The behaviors of the female were categorized into one of seven mutually exclusive categories (Table 1). Nursing, nosing, and positioning behaviors were analyzed both separately and as a combined category (interacting with pup, Table 1). Because both agonistic and reproductive behaviors represented time females spent interacting with conspecifics other than their pup, these behaviors were combined and analyzed as a single category (interacting with others, Table 1). To further characterize nursing behavior, we also examined nursing frequency and average nursing bout duration. Nursing frequency was estimated as the number of bouts recorded during an

Table 1. Definitions of behavioral categories used for the activity budgets of lactating gray seal (*Halichoerus grypus*) females.

Behavioral category	Definition
Interacting with pup	
Nursing	Pup is in contact with its mother's teat.
Nosing	Sniffing or rubbing of pup with snout.
Positioning	Rolling on side and presenting teats to pup or circling to move into nursing position.
Interacting with others	
Agonistic	Emitting a vocal threat toward, slapping fore-flipper against the body or clawing at, lunging at or biting another female, male or nonfilial pup.
Reproductive	Being mounted by or copulating with a male.
Resting	Sedentary and not engaging in one of the other behaviors.
Moving	Crawling or rolling not associated with one of the other behaviors.

observation session divided by the number of hours of observation. Switching of the pup between teats or off-teat breaks that were shorter than 10 s were included as part of one nursing bout. Because gray seal females are sedentary during nursing bouts, the proportion of total time females spent active was calculated as the percentage of the total observation time females spent engaged in behaviors other than resting or nursing. Comparisons across reproductive status (primiparous *vs*. multiparous) and lactation stage (early *vs*. peak) were analyzed using repeated-measures ANOVA with Bonferroni correction for multiple comparisons. Percentage values were arcsin transformed prior to analysis. All analyses were conducted in SPSS Version 11.0 (SPSS Inc., Chicago, IL). The nursing frequency (bouts/hour) of one primiparous female (peak lactation) and the nursing bout duration (min) of one multiparous female (peak lactation) were identified as extreme outliers with values >3 SD from the overall mean. Comparisons of nursing frequency and bout duration across reproductive status and lactation stage were conducted both with and without the outliers. Standard errors are reported throughout.

All sampling protocols were conducted in accordance with the requirements of the Canadian Council of Animal Care and were approved by the Department of Fisheries and Oceans Animal Care Committee (protocol numbers 04–02, 05–21, and 06–24).

Results

There were no significant differences in the total observation time of primiparous (early, $6.3 \pm 0.0.28$ h; peak, $6.0 \pm 0.0.26$ h) and multiparous (early, 5.7 ± 0.24 h; peak, 6.1 ± 0.17 h) females either by reproductive status ($P = 0.368$) or lactation stage ($P = 0.698$). The density of adults around primiparous (early, $0.016 \pm 0.0030/m^2$; peak, $0.012 \pm 0.0017/m^2$) and multiparous (early, $0.017 \pm 0.0028/m^2$; peak, $0.015 \pm 0.003/m^2$) females did not differ significantly by reproductive status ($P = 0.696$) or lactation stage ($P = 0.085$). Therefore, density was not considered further in the analysis.

Both primiparous and multiparous gray seal females spent the majority of their time resting followed by interacting with their pups, interacting with other conspecifics and moving (Table 2). The proportion of time females spent resting declined significantly between early and peak lactation in both primiparous and multiparous females (Table 2). Throughout lactation primiparous females spent significantly less time resting than multiparous females (Table 2). There was no significant difference in the proportion of time spent nosing or positioning between the groups or across lactation stages (Table 2). However, the proportion of time both primiparous and multiparous females spent nursing increased significantly between early and peak lactation (Table 2). Thus, the proportion of time females spent interacting with pups increased significantly between early and peak lactation in both groups. Although there was a trend for the proportion of time spent interacting with pups to be greater in primiparous females compared to multiparous females throughout lactation, the difference was not statistically significant. Neither the proportion of time spent interacting with others nor the time spent moving differed by reproductive status or lactation stage (Table 2). There were no significant interactions between reproductive status and lactation stage (Table 2).

Primiparous females spent significantly more time on average nursing than did multiparous females during both early and peak lactation (Table 2). Nursing frequency (bouts/hour) was significantly higher in primiparous females compared to multiparous females throughout lactation regardless of whether the single extreme outlier (primiparous female, peak lactation, Fig. 1A) was included ($P = 0.018$ and 0.046 for reproductive status and lactation stage, respectively) or excluded ($P = 0.023$ and 0.039 for reproductive status and lactation stage, respectively; Fig. 1A) from the analysis. Excluding the outlier, primiparous females engaged in nursing bouts more than twice as often as multiparous females during peak lactation (Fig. 1A). There was no significant interaction between lactation stage and reproductive status regardless of whether the outlier was included ($P = 0.068$) or excluded from the analysis ($P = 0.075$, Fig. 1A). The mean duration of nursing bouts did not differ by reproductive status or lactation stage regardless of whether the single extreme outlier (multiparous female, peak lactation, Fig. 1B) was included ($P = 0.155$ and 0.156 for reproductive status and lactation stage, respectively) or excluded ($P = 0.246$ and 0.278 for reproductive status and lactation stage, respectively; Fig. 1B) from the analysis. There were no significant interactions between lactation stage and reproductive status regardless of whether the outlier was included ($P = 0.135$) or excluded ($P = 0.223$, Fig. 1B) from the analysis. Thus, the significantly greater proportion of time spent nursing pups by primiparous females compared to multiparous females (Table 2) was a consequence of a significantly higher frequency of nursing bouts (Fig. 1B).

Although the proportion of time females spent active (total time − resting + nursing) tended to increase between early and peak lactation in both primiparous (early, 9.5 ± 1.84%; peak, 12.9 ± 2.52%) and multiparous females (early, 6.2 ± 1.14%; peak, 9.1 ± 2.35%), the increase was not significant ($P = 0.158$). The proportion of time spent active did differ between the groups, with primiparous females spending a significantly greater proportion of their time active compared to multiparous females throughout lactation ($P = 0.044$), however, the difference in activity corresponded to less than 4% of the overall time budget throughout lactation. There was no significant interaction between lactation stage and reproductive status ($P = 0.962$).

Table 2. Summary of the overall activity budget of primiparous ($n = 8$) and multiparous ($n = 8$) gray seal (*Halichoerus grypus*) females during early and peak lactation.

	Primiparous		Multiparous		*P*		
Behavior	Early	Peak	Early	Peak	Status	Stage	Status × Stage
Resting	84.1 ± 2.40	76.0 ± 2.87	90.0 ± 1.47	84.3 ± 2.21	**0.012**	**0.036**	0.789
Interacting with pup[a]	12.4 ± 2.33	17.8 ± 2.21	7.6 ± 1.22	11.1 ± 1.60	0.084	**0.021**	0.690
Nursing	6.4 ± 0.99	11.1 ± 1.38	3.8 ± 0.56	6.6 ± 0.90	**0.019**	**0.002**	0.510
Nosing	3.4 ± 1.38	4.8 ± 0.65	2.0 ± 0.44	3.4 ± 0.81	0.184	0.111	0.949
Positioning	2.6 ± 0.85	1.9 ± 0.56	1.8 ± 0.50	1.1 ± 0.25	0.211	0.166	0.929
Interacting with others[b]	2.7 ± 0.40	5.3 ± 3.23	1.9 ± 0.43	4.1 ± 2.35	0.489	0.437	0.894
Moving	0.8 ± 0.18	0.9 ± 0.10	0.5 ± 0.11	0.5 ± 0.11	0.093	0.892	0.337

Values are percentages of total observation time (mean ± standard error). Status: primiparous *vs.* multiparous, Stage: early *vs.* peak lactation. *P*-values in bold are statistically significant.

[a]Suckling, nosing, and positioning behaviors combined (see Table 1).

[b]Agonistic and reproductive behaviors combined (see Table 1).

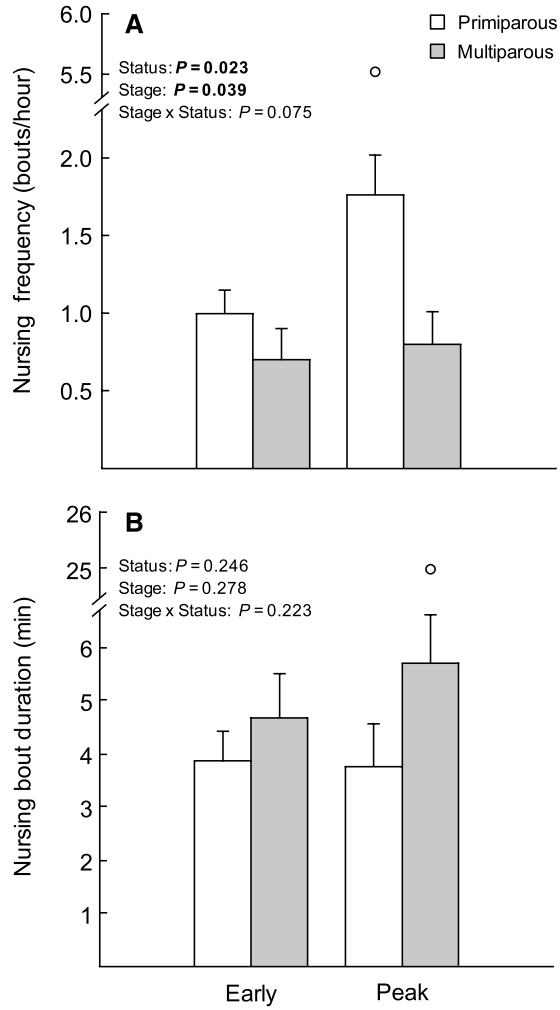

Figure 1. Nursing frequencies (A) and nursing bout durations (B) of primiparous ($n = 8$) and multiparous ($n = 8$) gray seal (*Halichoerus grypus*) females during early and peak lactation. Values are means ± standard errors excluding the extreme outliers (○, >3 SD from the mean). Status: primiparous *vs.* multiparous, Stage: early *vs.* peak lactation. Significance values are for repeated measures ANOVA with the extreme outliers excluded. *P*-values in bold are statistically significant.

Discussion

To our knowledge, this study is the first in a free-ranging mammal to compare the expression of maternal behaviors related to the transfer of milk energy to offspring between primiparous and multiparous females. As predicted, we found that primiparous gray seal females were significantly more active than multiparous females throughout lactation, however, the difference in activity represented only a small proportion of the overall time budget. Contrary to our

predictions, primiparous gray seal females spent as much time interacting with their pups as multiparous females and nursed more than multiparous females throughout lactation. These results suggest that a lack of prior reproductive experience does not substantially affect the expression of maternal behaviors in the gray seal.

The increase in the proportion of time spent nursing with lactation stage in both primiparous and multiparous females (Table 2) is consistent with previous behavioral observations in gray seals (Oftedal *et al.* 1987) and with measured increases in the daily milk intake of gray seal pups over the course of lactation (Mellish *et al.* 1999). Although both primiparous and multiparous females increased nursing effort over lactation, primiparous females spent more time on average nursing pups than multiparous females throughout lactation as a consequence of a significantly higher frequency of nursing bouts (Table 2, Fig. 1). Similar results have been observed for rhesus macaques (*Macaca mulatta*) in which primiparous females nursed their infants more frequently than multiparous females at all ages (Gomendio 1989). Studies in both domestic and laboratory species demonstrate that the mammary gland is not fully mature at first parturition and, as a result, primiparous females have a significantly lower rate of milk production over the course of lactation compared to multiparous females (Wada and Turner 1959, Vonderhaar *et al.* 1978, Fowler *et al.* 1990, Wagner *et al.* 2002). Increased suckling frequency by offspring in response to lower rates of milk output has been noted for a number of species (see Cameron 1998), suggesting that the higher nursing frequency observed in both primiparous gray seals and rhesus macaques may be a response to more frequent solicitation by offspring as a result of lower milk intake per nursing bout. Given that there were no significant differences in the proportion of time spent interacting with others (Table 2) or in the duration of nursing bouts between primiparous and multiparous females (Fig. 1B), it is unlikely that the higher frequency of nursing bouts observed in primiparous females was a consequence of a higher incidence of interrupted suckles due to disturbance by neighboring conspecifics.

Our results suggest that in contrast to observations in other species (*e.g.*, domestic sheep, *Ovis aries*, Alexander *et al.* 1993, Dwyer and Lawrence 2000; macaques, *Macaca fascicularis*, Timmermans and Vossen 1996 and *M. fuscata*, Tanaka 1989; prairie voles, *Microtus ochrogaster*, Wang and Novak 1994) maternal behaviors related directly to the care of the young are not less developed in primiparous gray seals. Although the difference was not significant, there was a trend toward primiparous females interacting more with their pups compared to multiparous females throughout lactation (Table 2), indicating that primiparous gray seal females were at least as attentive to their pups as multiparous females. The increase in the time spent nursing over lactation and the greater frequency of nursing bouts observed in primiparous females (Table 2, Fig. 1A) indicate that they are as responsive to the suckling demands of their pups as multiparous females throughout the lactation period. This may suggest that the neurological changes associated with a female's first reproductive effort (see Gonzalez-Mariscal and Poindron 2002, Numan *et al.* 2006) occur rapidly in gray seals, such that females are behaviorally fully prepared to care for their pups soon after first parturition. Thus, a lack of prior reproductive experience does not appear to have a substantial influence on the level of maternal care in gray seals. Our results suggest that a reduced time spent nursing offspring cannot account for the lower lactation performance observed in primiparous gray seals (Bowen *et al.* 2006). However, direct measures of both milk energy content and the rate of milk production (*e.g.*, Mellish *et al.* 1999) will be required to determine whether a reduced

physiological capacity for milk secretion in primiparous gray seal females may play a role.

Overall, the proportion of time females spent active during lactation was comparable to previous observations for gray seals (8.3%, Anderson and Harwood 1985). As predicted, primiparous females were more active than multiparous females throughout lactation (Table 2). The lack of a significant difference in the time spent interacting with others during either early or peak lactation between the groups (Table 2) suggests that, the difference in activity was not a consequence of differences in time spent engaged in agonistic or reproductive behaviors. Reproductive experience has been shown to attenuate the stress and fear responses of females (Wartella *et al.* 2003) suggesting that the higher level of activity in primiparous females may be a consequence of a greater sensitivity to the activities of neighboring conspecifics and, thus, a greater level of general alertness and activity. The difference in the time spent active between primiparous and multiparous gray seal females suggests that primiparous females may allocate a greater proportion of their initial energy stores to maternal maintenance costs *vs*. milk production and, thus, to pup growth. However, the difference in activity between the groups corresponds to less than 4% of the overall time budget on average. Although direct comparisons of the proportion of initial body energy stores allocated to milk production *vs*. maternal maintenance are needed (*e.g.*, Mellish *et al.* 1999), this relatively small difference suggests that higher activity levels of primiparous females may not have a major effect on their overall lactation performance.

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Literature Cited

Alexander, G., L. R. Bradley and D. Stevens. 1993. Effect of age and parity on maternal behaviour in single-bearing Merino ewes. Australian Journal of Experimental Agriculture 33:721–728.

Allen, P. J., W. Amos, P. P. Pomeroy and S. D. Twiss. 1995. Microsatellite variation in grey seals (*Halichoerus grypus*) shows evidence of genetic differentiation between two British breeding colonies. Molecular Ecology 4:653–662.

Anderson, S. S., and J. Harwood. 1985. Time budgets and topography: How energy reserves and terrain determine the breeding behaviour of grey seals. Animal Behaviour 33:1343–1348.

Boness, D. J., and H. James. 1979. Reproductive behavior of the grey seal (*Halichoerus grypus*) on Sable Island, Nova Scotia. Journal of Zoology London 188:477–500.

Boness, D. J., and W. D. Bowen. 1996. The evolution of maternal care in pinnipeds. Bioscience 46:645–654.

Bowen, W. D., W. T. Stobo and S. J. Smith. 1992. Mass changes of grey seal (*Halichoerus grypus*) pups on Sable Island: Differential maternal investment reconsidered. Journal of Zoology London 227:607–622.

Bowen, W. D., J. McMillan and R. Mohn. 2003. Sustained exponential population growth of grey seals at Sable Island, Nova Scotia. ICES Journal of Marine Science 60:1265–1274.

Bowen, W. D., S. J. Iverson, J. I. McMillan and D. J. Boness. 2006. Reproductive performance in grey seals: Age-related improvement and senescence in a capital breeder. Journal of Animal Ecology 75:1340–1351.

Bowen, W. D., J. I. McMillan and W. Blanchard. 2007. Reduced population growth of gray seals at Sable Island: Evidence from pup production and age of primiparity. Marine Mammal Science 23:48–64.

Broussard, D. R., T. S. Risch, F. S. Dobson and J. O. Murie. 2003. Senescence and age-related reproduction of female Columbian ground squirrels. Journal of Animal Ecology 72:212–219.

Cameron, E. Z. 1998. Is suckling behaviour a useful predictor of milk intake? Animal Behaviour 56:521–532.

Derocher, A. E., and I. Stirling. 1994. Age-specific reproductive performance of female polar bears (*Ursus maritimus*). Journal of Zoology London 234:527–536.

Dwyer, C. M., and A. B. Lawrence. 2000. Maternal behaviour in domestic sheep (*Ovis aries*): Constancy and change with maternal experience. Behaviour 137:1391–1413.

Fleming, A. S., and M. Li. 2002. Psychobiology of maternal behavior and its early determinants in nonhuman mammals. Pages 61–97 *in* M. H. Bornstein, ed. Handbook of parenting. Volume 2. Biology and ecology of parenting. Lawrence Erlbaum Associates, Mahwah, NJ.

Fowler, P. A., C. H. Knight, G. G. Cameron and M. A. Foster. 1990. In-vivo studies of mammary development in the goat using magnetic resonance imaging (MRI). Journal of Reproduction and Fertility 89:367–375.

Gittleman, J. L., and S. D. Thompson. 1988. Energy allocation in mammalian reproduction. American Zoologist 28:863–875.

Gomendio, M. 1989. Differences in suckling patterns between primiparous and multiparous rhesus mothers (*Macaca mulatta*). Journal of Reproduction and Fertility 87:529–542.

Gonzalez-Mariscal, G., and P. Poindron. 2002. Parental care in mammals: Immediate internal and sensory factors of control. Pages 215–298 *in* D. W. Pfaff, A. P. Arnold, A. M. Etgen, S. E. Fahrbach and R. T. Rubin, eds. Hormones, brain and behavior. Academic Press, San Diego, CA.

Hall, A. J., B. J. McConnell and R. J. Barker. 2001. Factors affecting first-year survival in grey seals and their implications for life history strategy. Journal of Animal Ecology 70:138–149.

Hall, A. J., B. J. McConnell and R. J. Barker. 2002. The effect of total immunoglobulin levels, mass and condition on the first-year survival of grey seal pups. Functional Ecology 16:462–474.

Iverson, S. J., W. D. Bowen, D. J. Boness and O. T. Oftedal. 1993. The effect of maternal size and milk energy output on pup growth in grey seals (*Halichoerus grypus*). Physiological Zoology 66:61–88.

Kinsley, C. H., R. Trainer, G. Stafisso-Sandoz, P. Quadros, L. Keyser-Marcus, C. Hearon, E. A. Amory-Meyers, N. Hester, M. Morgan, F. J. Kozub and K. G. Lambert. 2006. Motherhood and the hormones of pregnancy modify concentrations of hippocampal neuronal dendritic spines. Hormones and Behavior 49:131–142.

Maniscalco, J. M., K. R. Harris, S. Atkinson and P. Parker. 2007. Alloparenting in Steller sea lions (*Eumetopias jubatus*): Correlations with misdirected care and other observations. Journal of Ethology 25:125–131.

Mellish, J. E., S. J. Iverson and W. D. Bowen. 1999. Variation in milk production and lactation performance in grey seals and consequences for pup growth and weaning characteristics. Physiological and Biochemical Zoology 72:677–690.

Noren, S. R., D. Boness, S. J. Iverson, J. McMillan and W. D. Bowen. 2008. Body condition at weaning affects the duration of the postweaning fast in gray seal pups (*Halichoerus grypus*). Physiological and Biochemical Zoology 81:269–277.

Numan, M., A. S. Fleming and A. S. Levy. 2006. Maternal Behavior. Pages 1921–1993 *in* J. D. Neill, ed. Knobil and Neill's physiology of reproduction. Elsevier, St. Louis, MO.

Oftedal, O. T., D. J. Boness and R. A. Tedman. 1987. The behavior, physiology, and anatomy of lactation in the pinnipedia. Pages 175–245 *in* H. H. Genoways, ed. Current mammology. Volume 1. Plenum Publishing Corporation, New York, NY.

Pomeroy, P. P., S. D. Twiss and P. Redman. 2000. Philopatry, site fidelity and local kin associations within grey seal breeding colonies. Ethology 106:899–919.

Reiter, J., K. J. Panken and B. J. Le Boeuf. 1981. Female competition and reproductive success in northern elephant seals. Animal Behaviour 29:670–687.

Tanaka, I. 1989. Variability in the development of mother-infant relationships among free-ranging Japanese macaques. Primates 30:477–491.

Timmermans, P. J. A., and J. M. H. Vossen. 1996. The influence of repeated motherhood on periparturitional behavior in cynomolgus macaques (*Macaca fascicularis*). International Journal of Primatology 17:277–296.

Vonderhaar, B. K., G. H. Smith, R. J. Pauley, J. M. Rosen and Y. J. Topper. 1978. A difference between mammary epithelial cells from mature virgin and primiparous mice. Cancer Research 38:4059–4065.

Wada, H., and C. W. Turner. 1959. Effect of recurring pregnancy on mammary gland growth in mice. Journal of Dairy Science 42:1198–1202.

Wagner, K., C. A. Boulanger, M. D. Henry, M. Sgagias, L. Hennighausen and G. H. Smith. 2002. An adjunct mammary epithelial cell population in parous females: Its role in functional adaptation and tissue renewal. Development 129:1377–1386.

Wang, Z., and M. A. Novak. 1994. Parental care and litter development in primiparous and multiparous prairie voles (*Microtus ochrogaster*). Journal of Mammalogy 75:18–23.

Wartella, J., E. Amory, A. H. Macbeth, I. McNamara, L. Stevens, K. G. Lambert and C. H. Kinsley. 2003. Single or multiple reproductive experiences attenuate neurobehavioral stress and fear response in the female rat. Physiology and Behavior 79:373–381.

Weladji, R. B., A. Mysterud, O. Holand and D. Lenvik. 2002. Age-related reproductive effort in reindeer (*Rangifer tarandus*): Evidence of senescence. Oecologia 131:79–82.

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