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Individual size, sex, and rearing environment impact on aggression in newly weaned seals

KELLY J. ROBINSON AND PATRICK P. POMEROY, Sea Mammal Research Unit, Scottish Oceans Institute, University of St Andrews, St Andrews, Fife, KY16 8LB, United Kingdom; **NEIL HAZON,** Scottish Oceans Institute, University of St Andrews, East Sands, St Andrews, Fife, KY16 8LB, United Kingdom; **SIMON MOSS,** Sea Mammal Research Unit, Scottish Oceans Institute, University of St Andrews, St Andrews, Fife, KY16 8LB, United Kingdom; **SEAN D. TWISS,** School of Biological and Biomedical Sciences, Durham University, South Road, Durham, DH1 3LE, United Kingdom.

Aggressive behavior is an important aspect of an animal's behavioral repertoire when interacting with other conspecifics. The ability to defend oneself, a resource, or offspring from attack and to exploit opportunities to obtain food or territorial rights from others can have lifelong effects on the health, reproductive success, and survival of an individual (Campagna 2002). There is great variation in how aggressive different members of the same species are throughout the animal kingdom. Factors that can impact individual aggression include the age (Takahashi and Lore 1982), sex (Archer and Côté 2005), reproductive state (Rubenstein and Wikelski 2005), the genetic population from which they originate (Lahti *et al*. 2001), physical condition (Lucion *et al.* 1996), relative dominance ranking (Holekamp and Smale 1993), and personality type (Sih *et al.* 2004) of an individual. Alongside these individual traits, external factors such as the physical (DeVries *et al.* 2004) and social (Van Loo *et al.* 2001) environment have also been linked to variation in aggression. While there is much research on factors impacting on individual aggression, studying the ontogeny of aggression in infants in natural settings is crucial for understanding how individual aggressiveness develops.

Aggression in adult pinnipeds within certain contexts is well studied, most notably in competing males on breeding colonies (Campagna 2002). Conspecific

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[1] Corresponding author (e-mail: kjr33@st-andrews.ac.uk).

aggression in pinnipeds occurs in many contexts, including between adult males competing for access to females to mate (McCann 1981), between adult females with young pups and encroaching individuals (Boness *et al.* 1982) and on haul-outs outside the breeding season between individuals of different ages and sexes for space to rest (Sullivan 1982). However, no studies have investigated variation in aggressive behaviors in pinnipeds that are not competing for some kind of resource.

Newly weaned (Robinson *et al.* 2015) and adult male gray seals (Bishop *et al.* 2015) have previously shown significant individual differences in the amount of aggressive interactions they display towards other conspecifics. While gray seals have been shown to exhibit consistent individual differences (CID) in a variety of behaviors (Culloch 2012, Twiss *et al.* 2012), it is likely there are other underlying factors that affect how aggressive an individual is towards others, as the underlying developmental differences that cause CIDs are yet to be identified (Groothuis and Trillmich 2011). We investigated whether physical features (sex or size) and environmental factors (density of seals around the pup during rearing) affect the frequency of aggression seen when pairs of newly weaned gray seals are not competing over any resources, or whether this variation can be attributed solely to internal mechanisms promoting individual differences in aggressiveness.

This study took place on the Isle of May gray seal breeding colony in Scotland (56°11′N, 2°33′W) from 27 November to 5 December 2013. Twelve newly weaned gray seal pups were captured on the Isle of May in 2013 for our study. Gray seal mothers spend 18–20 d nursing their pups before abruptly weaning them, after which weaned pups spend 1–4 wk in a postweaning fast on the periphery of the breeding colony (Reilly 1991). Pups were defined as being weaned on the second consecutive day of being seen without their mother after a normal rearing period, based on daily observations (Bennett *et al.* 2007). All the study animals had weaned within 3 d of each other. Captured pups were placed into one of two holding pens to generate two groups of six individuals that had never encountered the individuals in the other pen. The sex ratio in the holding pens was even (three males and three females per pen).

Prior familiarity has been shown to decrease aggression between gray seals (Robinson *et al.* 2015), therefore we used individuals that had never previously encountered each other to avoid confounding the experiment. The use of newly weaned animals instead of adults allowed us to take advantage of the natural 1–4 wk postweaning fast in this species (Reilly 1991) and collection from different sites of the breeding colony ensures that individuals in the two separate pens had not encountered each other previously. Regular observations on study pups while still with their mothers at various sites scattered throughout the Isle of May breeding colony allowed us to be confident that individuals in one holding pen had not previously come into contact with the individuals in the other pen.

Upon capture all pups were sexed and weighed. Pups were weighed ±0.2 kg on a spring balance (Salter Industrial Measurements Ltd., West Bromwich, U.K.). Temporary paint marks were applied to all pups on the mid-dorsal region to assist individual identification. Pups <30 kg initially were excluded from the study. Criteria for early release from pens was set at animals falling below 30 kg or 75% of their capture mass, in accordance with previous studies using captive weaned gray seal pups to avoid extending the postweaning fasting period unnaturally (Bennett *et al.* 2007). None of the study animals lost sufficient mass to warrant early release. All pups were released into the wild after they participated in the study.

Pens were constructed as described in Robinson *et al.* (2015), with permission from Scottish National Heritage and in accordance with UK Home Office guidelines on suitable temporary holding facilities for gray seals, and were taken down once the trials were complete. Two types of pen were constructed; holding pens to house the pups outside of experiments and a single trial pen for use during the experiments. Holding pens were built utilizing stone walls already in place on the island and extended with wooden posts fenced with wire mesh. Both holding pens were 15 × 10 m and contained pools of fresh water. The trial pen was 5 × 5 m and out of sight from the holding pens. The trial pen was sufficiently large so that two weaned pups could be placed inside and could separate and not interact with each other if they chose to, so that neither individual would be competing solely for personal space during the experiment. The 12 newly weaned pups were penned in the holding pens for 8 d. After a day's rest postcapture to acclimate to the holding pens, experimental trials then commenced on the second day after capture.

Each trial occurred across 3 d. On day 1, a pair of seals that had not previously met was placed in the trial pen for 1 h (the "initial meeting"), using one animal from each holding pen. After the trial, participants were separated and returned to their original holding pen. After a rest day, on the third day of the trial the same two individuals were placed in the trial pen for another hour (the "second meeting"), after which they were returned to their original holding pens. The use of the same pairing of individuals twice enabled us to control for individual responses to specific individuals within the study group, and the consistency of the frequency of behaviors across the two trials was investigated to ensure familiarity with the other trial individual was not affecting the results of the experiment. No individual was used in more than one trial per day and pups had a rest day between each trial day.

The two subjects required for a trial were captured in the holding pens simultaneously and transported while restrained in a bag to the trial pen at the same time. Time spent capturing and transferring pups from the holding pen to the trial pen was always under 3 min. The animals were introduced into the trial pen simultaneously in a standardized manner. Both of the hour long periods of time spent in the trial pen were recorded (video camera used: Panasonic HDC-TM60 HD 1920 × 1080) from a hide. Six trials were run per day with all study pups being used once per trial day. Twenty-four trials took place over 8 d of captivity, each consisting of an initial meeting trial and a second meeting trial with a rest day in between (n = 48 individual trial responses, 24 initial meetings, and 24 second meetings). Although the same individuals were used for multiple trials across their period in captivity, the same pairs of individuals were never recreated outside of the initial and second meetings in any subsequent trials.

Real-time video footage was decoded after all trials were completed using an ethogram from Robinson *et al.* (2015) to produce two metrics for analysis: (1) frequencies of each behavior type (Affiliative, Olfactory, and Visual investigative behaviors ("checks") or Aggressive interactions between the trial animals) and (2) the cumulative time in seconds spent within a threshold distance of one body length of each other. All distances were estimated visually in multiples of weaned pup length, which equates to approximately 1 m. Adult gray seals typically maintain distances of approximately two adult body lengths (*ca.* 4 m) between themselves and neighbors on breeding colonies, and interactions between adults tend to only take place between individuals within that range (Redman 2002). We assume any individual within one body length of another would be sufficiently close to evoke a response from subjects that have never previously encountered each other. The most extreme reaction possible to another individual in the trial was biting, and no bites that perforated the skin occurred in any of our trials. To ensure animal welfare was not compromised during the study all trials were observed by a researcher who could intervene and separate subjects if necessary during a trial. This was not required during the study.

One investigator (KJR) decoded all the videos for this study. Their standard error was calculated by decoding six different videos twice. Across the six videos, standard errors for tallied frequencies of behaviors ranged from 0 to 2 per video and for cumulative time spent within one body length in trials ranged from 1 to 31 s.

All analysis was performed using the statistical package R 2.15.0 (R Development Core Team 2012). A generalized additive mixed model (GAMM) (Wood 2006*a*) was generated to investigate whether a variety of individual characteristics significantly affect frequencies of aggressive interactions. Biologically plausible predictor variables considered for inclusion in this model was the sex of the focal individual, the time spent in captivity in days, the size of the focal individual (mass in kilograms at capture) and the density of conspecifics in the region the pup was raised on the breeding colony, or "rearing environment" ("High" or "Low," $n = 6$ for each). The high and low density colony sites were defined based on counts of the numbers of seals in the same area of land at the two different locations on the colony. The high density part of the colony had approximately three times the number of seals than the low density part of the colony across the same area of land (96 compared to 34 individuals, respectively). The mass of each individual on the day of each trial was not used because weaned pups lose mass daily during the postweaning fast, making the mass measurements throughout the trials and the "time in captivity" highly correlated. To avoid this, mass at capture was used for all trials to define an individual's size, as within the study group the size of an individual relative to the others remained consistent throughout the study period (*e.g.*, the largest at the start was the largest at the end). Size was fitted as a smooth term with an interaction with sex. The identities of the response individual in the trials were fitted as a random effect smooth (Wood 2006*b*) to control for potential consistent individual differences in the behavior of the response individual (Culloch 2012, Twiss *et al.* 2012). The smooth for focal individual was not included in this model as all predictor variables contained information about the focal individual. The model was fitted with a Poisson error distribution with log links using the multiple generalized cross validation library mgcv (Wood 2012).

To determine whether familiarity between the two individuals used across one trial was impacting on their behaviors, four GAMMs were used to investigate the consistency of the following response variables, which have been previously shown to change with familiarity (Robinson *et al.* 2015): (1) the frequency of affiliation, checks and aggressive interactions and (2) the total cumulative number of seconds animals spent within one body length of each other. Biologically plausible predictor variables considered for inclusion in these models were the sex of the focal individual and time spent in captivity in days. The identities of both individuals in the trials were fitted as two random effect smoothes (focal and response animal) (Wood 2006*b*) to control for pseudoreplication in the data set due to use of the same individuals in multiple trials and to control for consistent individual differences in behavior. The models of the frequencies of aggressive interactions and affiliation behaviors within the 1 h trial were fitted with Poisson error distributions with log links using the multiple generalized cross validation library mgcv (Wood 2012). The models of time spent within one body length and frequency of checks were fitted with Gaussian distributions.

For all models, the smoothing parameters were set by maximum likelihood to reduce the risk of overfitting associated with other methods (Wood 2011). Each model's goodness of fit was examined by calculating R^2 values, AIC scores, QQ, and residual plots.

The frequency of aggressive interactions was significantly affected by the smooth term for size and sex interaction ($P < 0.001$), the rearing environment ($P < 0.001$), time in captivity ($P < 0.001$) and the individual identity of the response individual ($P \leq 0.001$) (Table 1). The effect an individual's size had on aggression frequencies in our trials was highly dependent on the sex of an individual. Males showed a positive linear relationship between size and aggression frquency, while female individuals had a nonlinear relationship between size and aggression (Fig. 1 and 2, respectively). There were fewer aggressive interactions as time in captivity increased and individuals raised in a high density area of the breeding colony exhibited more aggression than those raised in low density areas (Table 1).

Familiarity did not affect the behavior of trial individuals across the 2 d trial. The frequency of Checks (GAMM: $R^2 = 0.2$, $P = 0.3$), Aggressive interactions (GAMM: $R^2 = 0.4$, $P = 0.4$), Affiliative behaviors (GAMM: $R^2 = 0.6$, $P = 0.06$) and the time spent within one body length (GAMM: $R^2 = 0.43$, $P = 0.5$) were not significantly different across the initial or second meeting (Table 2).

Our study has identified several individual variables that influence aggression frequency between weaned gray seal pups who have never met and who are not competing for a resource. We show that a combination of physical and environmental variables can affect aggressive behavior, and could contribute to how CIDs manifest within an individual. While these findings come from only 12 individuals, they may indicate individual covariates that are worth investigating in future studies.

In our study group, male weaned pups showed more aggression the larger they were compared to other individuals. This could be an early expression of behavioral strategies seen in adults, as an adult male's size, dominance ranking, and aggression frequencies have been linked to each other and to mating success in several phocid species (gray seals: Anderson and Fedak 1985, Godsell 1991, Lidgard *et al.* 2012; harbor seal: Sullivan 1982; southern elephant seal, *Mirounga leonina*: McCann 1981, Modig 1996; northern elephant seal, *Mirounga angustirostris*: Haley *et al.* 1994). However, the males in our study were approximately 8 yr away from the age they would typically first be able to hold tenure on a breeding colony (Godsell 1991).

Table 1. Model output from the GAMM analyzing aggression frequencies and individual variables in recognition trials with their estimates, standard errors, and *P*-values, including all smooth terms with their standard deviations and *P*-values.

Model: response variable	Predictor variables	Estimate	SE	*P*-value
Aggressive interactions	Time in captivity	−0.12	0.02	<0.001
	Rearing environment (High/Low)	−3.8	0.84	<0.001
	Smooth terms		SD	*P*-value
	Mass at capture (kg) and sex interaction (female)		1.8	<0.001
	Mass at capture (kg) and sex interaction (male)		1.05	<0.001
	Random effect smooth term for response individual identity		0.79	<0.001

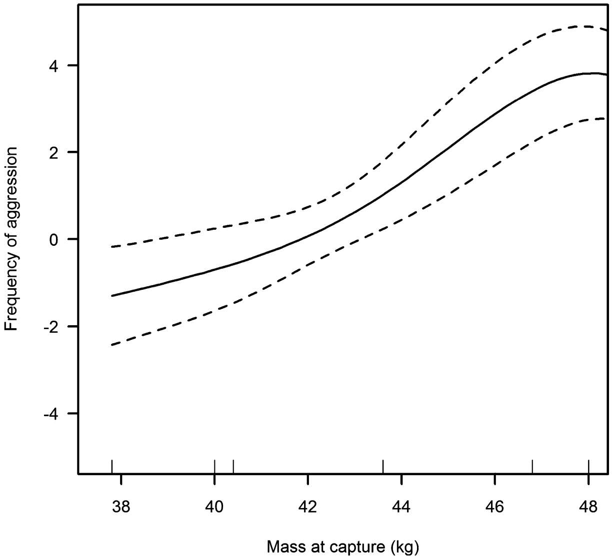

Figure 1. Frequency of aggression (smooth based on size by sex interaction on a linear scale predictor) from newly weaned male gray seals (*n* = 6) and their size (mass at capture in kilograms) with confidence intervals (dashed) and data points shown on the *x*-axis.

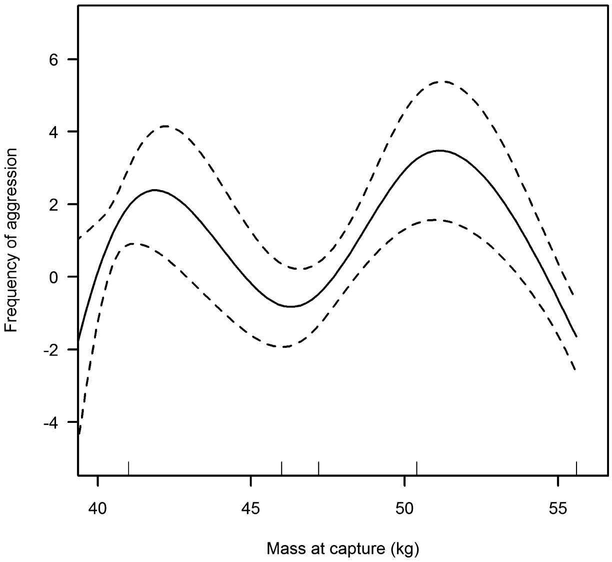

Figure 2. Frequency of aggression (smooth based on size by sex interaction on a linear scale predictor) from newly weaned female gray seals (*n* = 6) and their size (mass at capture in kilograms) with confidence intervals (dashed) and data points shown on the *x*-axis (two individuals were the same mass at capture, hence only five points).

Table 2. Mean values (with standard errors) for the frequencies of Affiliative behavior, Checks, Aggressive interactions, and the time spent within one body length of the response animal for each type of trial.

Trial type	Affiliative behaviors (per hour)	Checks (per hour)	Aggressive interactions (per hour)	Time within one body length (hours:minutes:seconds)
Initial meeting ($n = 24$)	4.2 ± 0.3	79.2 ± 6.8	25.9 ± 0.4)	00:39:15 ± 00:05:07
Second meeting ($n = 24$)	2.9 ± 0.2	70.5 ± 7.9	23.2 ± 0.07	00:34:38 ± 00:04:18

Therefore, it would be interesting to determine if an individual's size and/or aggressiveness remained consistent during this period or if they changed depending on body condition or the conspecifics surrounding them. Additionally, as our definition of "size" was based on mass, and as all trial individuals were experiencing a postweaning fast when the experiments took place, we cannot rule out small males acting passively due to limited energy resources as an individual's size on departing the colony significantly impacts their likelihood of first year survival (Hall *et al.* 2001).

The density of conspecifics around the pup while with its mother for the 18 d dependent period had a significant impact on the aggression frequencies our trial individuals exhibited. Individuals raised in low density areas of the breeding colony exhibited less aggression in trials than those raised in high density areas of the colony. There are several potential explanations for this result in gray seals. Mothers rearing pups in high density areas of the breeding colony must defend themselves from encroaching individuals more regularly, exposing their pups to more aggressive interactions (Pomeroy *et al.* 2000). There has been a long history of studies investigating the impacts of early social environment on an infant's subsequent behavior in a wide range of animal species, from ants to nonhuman primates (reviewed in Scott 1962). The social environment in which an individual is raised has been shown to exert lifelong effects on adult behavior (Crawley *et al.* 1975, Takahashi 1986) and reproductive success (Berger *et al.* 2015). However, the source of this variation may also be genetic, as high density sites on breeding colonies are frequently occupied by aggressive, dominant males (Boness *et al.* 1982) and females (Pomeroy *et al.* 2000). Further research is needed to determine whether heightened aggressiveness in high density reared infants persists into adulthood, whether it is consistent throughout an individual's lifetime, or if this relationship is present in other age groups or species.

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