# Chapter 9. Gray seals: 80 years of insight into intrinsic and extrinsic drivers of phocid behavior.

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### Frontice piece

Some early behavioral observations of gray seals from 'Martin Martin:  A Description Of The Western Islands Of Scotland Circa 1695*' (Concerning a debate on the eating of seals);

> "*a debate between a Protestant gentleman and a Papist of my acquaintance : the former alleged that the other had transgressed the rules of his church, by eating flesh in Lent: the latter answered that he did not ; for, says he, I have eat a sea-creature, which only lives and feeds upon fish. The Protestant replied, that this creature is amphibious, lies, creeps, eats sleeps, and so spends much of its time on land, which no fish can do and live. It hath also another faculty that no fish has, that is, it breaks wind backward so loudly, that one may hear it at a great distance*."

* Edited by D.J. Macleod, Birlinn Ltd, 1994

## Abstract

The gray seal is a data-rich species with behavioral studies dating back to the 1940s. The reasons for the wealth of knowledge are partly fortuitous; pioneering naturalists ventured forth to remote island colonies around the UK and Canada to observe the 'hook-nosed sea-pig' during their annual breeding seasons. These early qualitative treatises on gray seal behavior ignited further, more quantitative, research interest, which has continued to expand to this day. Several gray seal traits enhance its suitability as a study system for understanding drivers of behavior, such as their ease of observation and site-fidelity during breeding, and unique pelage patterns enabling the collection of long-term data on known individuals. Gray seals also inhabit a remarkable variety of habitats, both on land and at sea, facilitating comparative studies of environmental drivers of behavior. These traits have enabled pioneering behavioral research across a wide range of life-history stages. This chapter aims to capture the diversity of behavioral knowledge derived from gray seals, revealing how they interact with one another and their environment. We also highlight new research areas likely to present research opportunities and challenges in the near future, especially in the context of rapidly changing terrestrial and marine environments.

## Keywords

*Halichoerus grypus*, social interactions, maternal care, polygyny, mating patterns, foraging behavior, novel behaviors, individual differences, personality.

## 9.1 Introduction

There is a long and productive history of research on gray seals (*Halichoerus grypus*) in both the Eastern and Western Atlantic populations, encompassing demography, life-history, reproduction, and foraging ecology. Behavioral studies are integral to a thorough understanding of gray seal biology and feed into all aspects of gray seal research. In this chapter, we focus on research where ethological aspects are foremost, or where behavioral observations have resolved outstanding questions, provided new insights, or indeed, highlighted new paths for scientists to explore.

Behavior is essentially about interactions between individuals and their environment, whether abiotic or biotic, including conspecifics and heterospecifics. Therefore, one should not view behavior in isolation. One needs to quantify the context of behavior at an appropriate biologically relevant spatial, temporal, or social scale (or scales), to get at the meaning of, and scope for, behavioral choices. Ideally, this should link with information on energetic and physiological constraints that set the intrinsic scope for behavior within and across individuals (Chaps. 4 and 8). As behavior is basically about interactions, it seems artificial to impose a chapter structure that separates males, females, juveniles, and pups. For example, male-male interactions are inevitably modified by the availability of sexually receptive females. However, there are some key areas of gray seal behavior that have been studied in detail and that illustrate these interactions well: male-male reproductive competition, female-pup interactions, and female–habitat interactions. We deal with these interactions, then look at some new avenues emerging in the literature and consider potentially valuable future directions to promote a deeper understanding of the behavior of gray seals, if certain practical considerations can be overcome. First, however, we reflect on the long history of gray seal ethological studies, with the aims of illustrating the development of gray seal behavioral research, and how the qualities of this system have allowed researchers to contribute to the wealth of knowledge about gray seals, making this a ‘data-rich’ species.

## 9.2 History

Early ethological studies of gray seals centered on terrestrial life-history phases, and in particular, breeding behavior. Gray seal colonial breeding behavior provides excellent observational access to breeding adults, pups of the year, and in some cases, juveniles of pre-breeding age. Consequently, most gray seal ethology is conducted on wild populations rather than captive individuals. This has the advantage of allowing examination of behavior in the context of natural selective pressures under which seals operate, though limiting the scope for experimental manipulation of behavior. Frank Fraser-Darling pioneered ethological observations of breeding gray seals based on his prolonged stay on the North Rona (Scotland, UK) colony (Fraser-Darling 1939) that described much of the basic breeding behavior of gray seals. In the 1950s, other intrepid researchers followed Fraser-Darling's example. They ventured to various UK colonies during the autumn breeding season, providing detailed descriptive, but often rather anecdotal, accounts of behavior (e.g., Davies 1949, Matthews 1950, Hewer 1957, 1960, Fogden 1971) that are engagingly collected in a book by Hewer (1974) along with his extensive observations. In the Western Atlantic, Cameron (1967, 1969, 1970) braved winter conditions to provide comparative behavioral descriptions of gray seals that breed in mid-winter. The 1960s also saw a growth in more quantitative studies among Eastern Atlantic gray seal populations (e.g., Hewer and Backhouse 1960, Boyd and Laws 1962, Boyd et al. 1962, Coulson and Hickling 1961, 1964), which focused primarily on establishing basic population parameters, such as the timing of breeding, numbers of seals, sex ratios, pup production, and mortality with the aim of understanding the drivers of population dynamics. The ethological aspects of these studies remained largely anecdotal and descriptive. It was not until the mid-1970s that extensive, formally structured quantitative behavioral observations came to the fore as a key component of gray seal biology. Studies such as those by Anderson et al. (1975), Burton et al. (1975), and Anderson and Fedak (1985) followed known individuals on North Rona (Scotland, UK). Parallel studies of the Western Atlantic gray seal population at Sable Island (Canada) provided valuable comparisons across populations (e.g., Boness and James 1979, Miller and Boness 1979, Boness et al. 1982, Boness 1984). These studies integrated behavioral information about specific individuals into the broader breeding biology of gray seals. They framed their research in the context of emerging theories within behavioral and evolutionary ecology, such as drivers of variation in female and male lifetime reproductive success. Much of this early behavioral focus was on mother-pup interactions, with a particular interest in maternal investment and pup development, again primarily with a focus on the impacts at the level of the population. Studies elsewhere complemented these efforts, with Kovacs (1987) producing detailed ethological work on mothers and pups on the Isle of May (Scotland, UK) colony.

These foundational quantitative ethological studies of breeding gray seals established a route that many have followed, exploring in detail the processes that drive patterns of behavior. The breadth and depth of understanding of gray seal behavior have been extended by the integration of new research techniques from emerging disciplines, such a molecular ecology (Ambs et al. 1999, Amos et al. 1993, 1995, 2001, Allen et al. 1995, Boskovic et al. 1996, Perry et al. 1998, Worthington-Wilmer et al. 2000, Pomeroy et al. 2001, Bean et al. 2004, Twiss et al. 2006, Tollit et al. 2009) and spatial ecology (e.g., Twiss et al. 2000, Pomeroy et al. 2001, Stewart et al. 2014); and by asking questions from emerging perspectives such as the concept of animal personalities (Twiss and Franklin 2010, Twiss et al. 2012a, Twiss et al. 2020). Throughout much of this research, a notable strength of the gray seal study system has been the ability to identify individuals consistently across successive encounters (e.g., breeding seasons), enabling detailed longitudinal studies of known individuals (e.g., Pomeroy et al., 1999, Bubac et al. 2018, Weitzman et al., 2017). In earlier studies, identification was primarily by artificial marks (e.g., flippers tags, brands). However, with the advent of more dedicated ethological studies, pelage patterns were used by skilled observers as a reliable and non-invasive means to recognize known individuals (Redman et al. 2001). This process came into much wider use with the application of digital photography and the development of computer-aided matching (e.g., Hiby and Lovell 1990, Vincent et al. 2001, Karlsson et al. 2005, Gerondeau et al. 2007, Hiby et al. 2013). The ability to reliably identify known individuals has yielded new insights into individual differences in behavior (e.g., Twiss and Franklin 2010, Twiss et al. 2012a, Bubac et al. 2018). Consequently, ethological studies of gray seals are asking ever more detailed behavioral questions, particularly at the level of within population and individual variation; delving into the mechanisms underlying mother-pup interactions (e.g., Robinson et al. 2015a, 2019), male competitive and mating behavior (e.g., Bishop et al. 2014, 2015a, b, Lidgard et al. 2012), female mate choice (Amos et al. 1995, 2001, Ambs et al. 1999, Twiss et al. 2006), social associations (e.g., Pomeroy et al. 2005), fine scale environmental drivers of habitat use (e.g., Twiss et al. 2000, Pomeroy et al. 2001, Matthiopoulos et al. 2005, Stewart et al. 2014) and how behavior responds to environmental change (e.g., Twiss et al. 2007, Weitzman et al. 2017).

The depth and breadth of ethological research into gray seals has shown that long-term behavioral observations are integral to understanding the biology and life-history of breeding seals. Among the Eastern and Western Atlantic gray seal populations, the breeding colonies of North Rona and the Isle of May off the Scottish coast, and Sable Island off the Canadian East coast, have been three of the most important long-term study sites yielding much of the behavioral research on breeding gray seals. In more recent years, these long-term study sites have been complemented by a growing number of behavioral studies among populations and colonies in different contexts and habitats. For example, cave breeding seals around the UK coast (e.g., Leeney et al. 2010), land-fast and pack ice breeding colonies (e.g., Lydersen et al. 1994, Haller et al. 1996), seals in the Baltic that alternate between land and ice breeding habitats dependent upon prevailing weather conditions (Karlsson et al. 2005, Jussi et al. 2008), and newly emerging study sites as populations of gray seals shift over time, such as parts of the North Sea (e.g., Reijnders et al. 1995, Bishop et al. 2014, Abt and Engler 2009, Brasseur et al. 2015), Greenland (Rosing-Asvid et al. 2010) and the Northeast US coast (Lerner et al. 2018).

Breeding is only part of the life-history of a gray seal. While the annual breeding attempt is arguably the culmination of the previous year's foraging effort, understanding the behavior of gray seals at sea is also critical. Gathering such data has been challenging due to limited opportunities to directly observe seals at sea, and especially to observe interactions between individuals, an essential aspect of behavioral studies. Observational studies at non-breeding haul-out sites can provide some insights into at-sea behavior patterns, in particualr spatial and temporal movement patterns between haul-outs  (e.g., Karlsson et al. 2005, Leeney et al. 2010, Sjöberg and Ball 2000, Survilienė et al. 2016). However, it is the application of biotelemetry devices that has revolutionised our understanding of gray seal behavior at sea (Chap. 6), though such 'behavior' is typically inferred from indirect measures such as space use (e.g., Thompson et al. 1991, McConnell et al. 1992, 1999, Beck et al. 2000, Lidgard et al. 2003, Austin et al. 2004, Harvey et al. 2008, Breed et al. 2009, Cronin et al. 2012, Carter et al. 2016) and motion (e.g., Shuert et al. 2018). Being dependent upon expensive technology, studies at sea can suffer from more restricted  sample sizes than observational studies of seals on land (Hazekamp et al. 2010). However, the wealth of biotelemetry studies of gray seals provides some of the most comprehensive and informative insights into what seals are capable of once they disappear under the waves (Chapt 6).

Our overview of gray seal ethology starts by examining behavior during the main terrestrial phase of the gray seal lifecycle: the breeding season. We then head underwater and explore the insights provided by a growing number of studies that track seals at sea. Finally, we focus on some intriguing and challenging emerging areas of gray seal ethological research, aiming to highlight potentially fruitful, but certainly exciting, avenues for future research.

## 9.3. Interactions on Land: The Breeding Season

### *9.3.1 Interactions Among Males*

Male gray seals reach sexual maturity at 2.6 years of age, but social maturity, in terms of achieving reproductive success, typically is not achieved until 8–10 years (Hammill and Gosselin 1995). There are two predominant behavioral phenotypes, or reproductive strategies, exhibited by male gray seals during the breeding season (Anderson et al. 1975, Boness 1984, Anderson and Fedak 1985, Twiss et al. 1994, Lidgard et al. 2005, Bishop et al. 2015b). Males that maintain access to females in a “come early and stay long" strategy are typically classified as ‘tenured’. In contrast, males that remain on the periphery of the colony, roaming and attempting to mate with females opportunistically, are considered ‘transient’ (Boness and James 1979, Lidgard et al. 2001, Lidgard et al. 2005). Although the length of tenure varies among individuals, tenured males can remain on the breeding colony for up to 60 days and fast throughout this time (Boness and James 1979, Anderson and Fedak 1985, Twiss 1991, Lidgard et al. 2003, Bishop et al. 2017). While there is some evidence of aquatic mating, there is debate whether this represents a third discrete mating strategy or is an extension of the opportunistic transient strategy (Gemmell et al. 2001, Lidgard et al. 2005, Twiss et al. 2006). The relative success of transient and tenured strategies has been assessed at several colonies (Amos et al. 1993, Twiss et al. 1998, 2006, 2007, Ambs et al. 1999, Worthington-Wilmer et al. 1999, Lidgard et al. 2001, 2004, Bishop et al. 2017). Most studies rely on visual observations of consortship or copulations as measures of male success, and there are likely to be discrepancies between observed mating success and realized reproductive success, i.e., fertilizations (Amos et al. 1993, Ambs et al. 1999, Worthington-Wilmer et al. 1999, Lidgard et al. 2004, Twiss et al. 2006). There is evidence of significant polygynous reproductive skew at most gray seal colonies, with tenured males having a high probability of fertilization relative to transient males (Lidgard et al. 2004, Twiss et al. 2006).

During the breeding season, tenured males engage in agonistic interactions to defend non-exclusive, often loosely defined territories in which they attempt to maintain position among shifting groups of females (Anderson et al. 1975, Boness and James 1979, Twiss et al. 1994). Males engage in two forms of agonistic contest interactions. Non-contact interactions consist of open-mouth threats (Miller and Boness 1979, Boness 1984), rolls (Cameron 1967), and other posturing behaviors (Boness and James 1979, Bishop 2015, Bishop et al. 2014; Fig. 9.1). In cases where two males are similarly matched or neither retreats after such exchanges of threats, then aggression can escalate, taking the form of contact interactions or fights. Contact interactions consist of males exchanging bites and lunges to each other’s neck and wrestling (Fig. 9.1). Fights typically conclude when a winner maneuvers and is able to bite, or threaten to bite, the opponent’s hind flippers or tail or when one combatant begins to back away in an attempt to turn and flee, often pursued by the other and chased out of the area (Boness and James 1979, Twiss 1991, Bishop 2015). Very rarely does a contest end in a mortal injury (Miller 1991). This pattern of escalating interactions is generally well-conserved across other polygynous, sexually size-dimorphic pinnipeds (Miller 1991). However, for gray seals, 23–60% of non-contact and contact interactions result in a draw outcome, where neither male cedes position, which results in non-linear dominance hierarchies (Anderson and Fedak 1985, Tinker et al. 1995, Twiss et al. 1998, Bishop et al. 2015b, Fig. 9.2). This behavioral mechanism of ‘not losing’ for gray seals is linked with mating success (Anderson and Fedak 1985), but how individuals make decisions during contests regarding whether to de-escalate, settle for a draw, or push for a win-lose outcome is poorly understood. Considering that many studies of animal contests do not even mention draws as a possible outcome (e.g., Haley 1994, O’Donnell 1998, Colléter and Brown 2011), the gray seal system represents a prime opportunity to explore a relatively understudied facet of animal decision making, game theory, and information gathering (Riechert and Hedrick 1993, Whiting 1999, Carlin et al. 2005, Whiting et al. 2006, Bishop 2015).

**Fig. 9.1.** The most ubiquitous threat display for male gray seals is the non-vocal open-mouth threat wherein a male opens his mouth to a wide gape oriented towards or perpendicular to opponent (a-b). When contests escalate into an interaction with physical contact, males exchange lunges and bites during bouts of wrestling (c-d). Both males typically attempt to maneuver towards his opponent’s hind flippers or tail. The male that successfully bites his opponents’ hind flippers is usually, but not exclusively, the winner of the interaction. Image credits: AM Bishop.

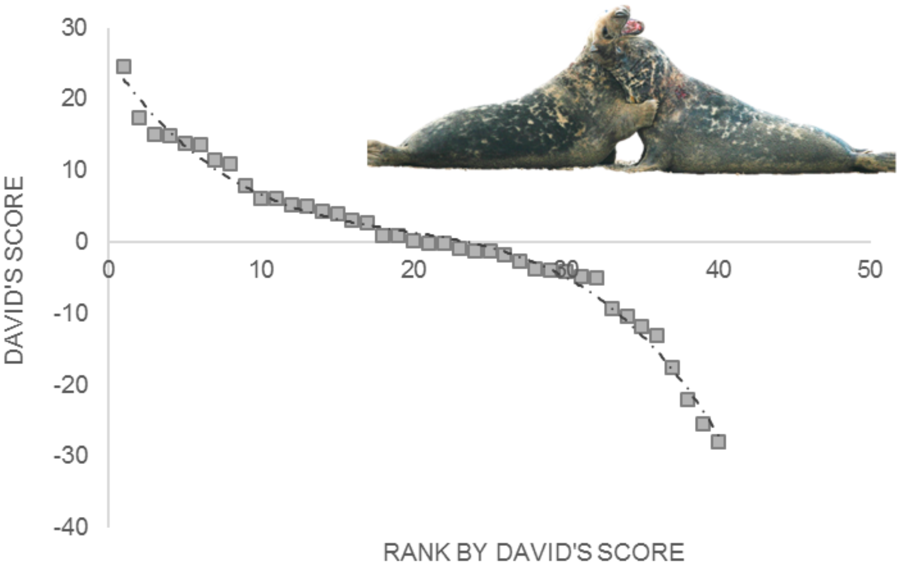


**Fig. 9.2.** An example of the non-linear male dominance hierarchy from Donna Nook breeding colony, England (Bishop 2015). Individual males' dominance scores were calculated using David's Score where high positive values represent high dominance (Gammell et al. 2003, de Vries et al. 2006) and included the outcome of draws. Apart from a few clearly dominant and subordinate individuals, most males have similar dominance scores. Similar hierarchy structures have been identified at North Rona, Scotland (Twiss et al. 1998). Image credits: AM Bishop.

In addition to observing patterns of behavioral interactions, considerable work has been carried out to link intrinsic and extrinsic factors with male success. For example, like other sexually size-dimorphic pinnipeds (Bartholomew 1970, Chaps. 7 and 11), the 'tenured' male gray seal strategy is typically adopted by older and larger individuals (Anderson and Fedak 1985, Godsell 1991, Carlini et al. 2006, Lidgard et al. 2012). Within this category, there is some evidence that larger males are more likely to win fights and maintain their position (Anderson and Fedak 1985). However, linked to the prevalence of draws was the finding that 'not losing' is more important than winning (Anderson and Fedak 1985), and males that can stay longer on a breeding colony have more matings and, therefore, overall reproductive success (Anderson et al. 1975, Anderson and Fedak 1985, Lidgard et al. 2005, Twiss et al. 2006, Bishop et al. 2017). To maximize length of stay, stabilizing selection has likely favored individual tenured males that achieve a fine balance between energy conservation (by minimizing activity) and the importance of not losing position among females. This trade-off between endurance for long tenure and agility during fights is evidenced by the findings that 60–90% of male time on breeding colonies (whether land or ice) is spent resting or idle (Boness 1984, Twiss 1991, Tinker et al. 1995, Bishop et al. 2015c), and by the inverted ‘U’ shape relationship between size and mating success observed on Sable Island, in which intermediate-sized males were most successful (Lidgard et al. 2005).

Extrinsic factors also influence the underlying relationship between the length of tenure and reproductive success. Colony topography and environmental factors (see 9.3.6) can play a role in the behavioral mechanisms required to achieve extended stay, such as the necessary levels of aggression, which in turn can shape the degree of polygyny (Anderson and Harwood 1985, Twiss et al. 1998, Bishop et al. 2015b). Gray seals breed on a variety of substrates, including rock, sand, and ice (Stirling 1975, Boness and James 1979, Anderson and Harwood 1985, Tinker et al. 1995, Twiss et al. 1998, Bishop et al. 2015b). On colonies with open access and wide, uniform, tidal beach topography, sex-ratios are typically less skewed, and individual tenured males engage in more aggressive interactions per day compared to males at colonies with restricted access and heterogeneous topographic features (Twiss et al. 1998, Fig. 9.3). Local neighborhood social stability has also been linked to a reduced number of aggressive interactions at the individual level. However, the localized stability experienced by individuals can be disrupted by environmental perturbations such as tidal surges or storms (Bishop et al. 2015b). Thus, while historical studies at long-term monitoring sites provide a valuable baseline, it will be essential to track how male-male behaviors and subsequent colony dynamics respond under current environmental conditions, particularly relative to predictions of increased stochasticity in weather related to global climate change.

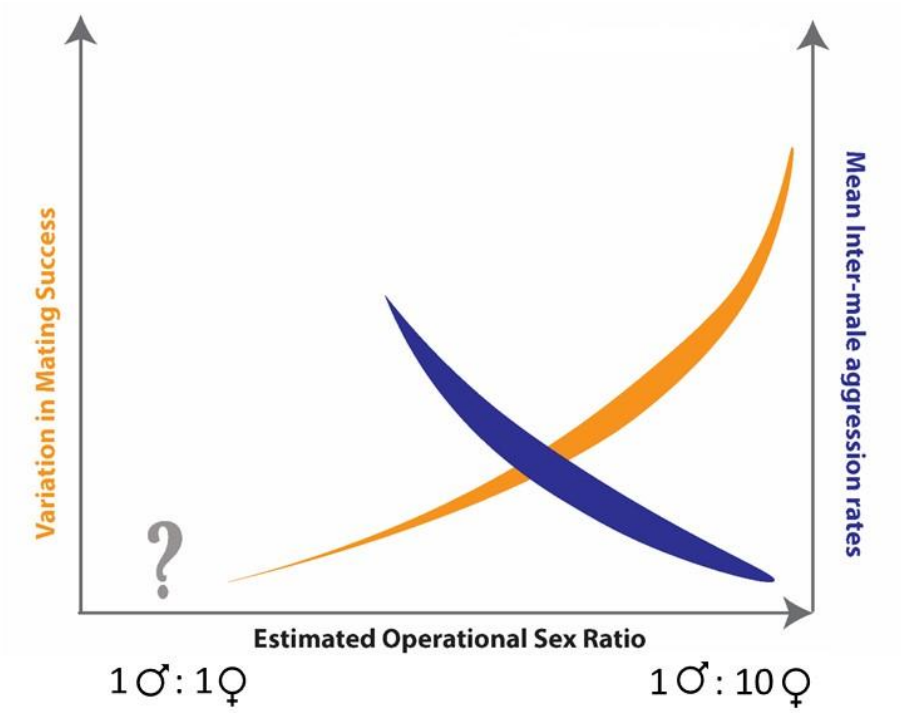


**Fig. 9.3.** Schematic illustrating the general relationships between operational sex ratio on breeding colonies (the average number of reproductive females per male) and the degree of variation in male mating success and the average levels of male-male aggression. Operational sex ratio is strongly influenced by the physical structure of the colony in terms of access to/from the sea and the degree of female aggregation driven by the availability of suitable pupping habitat within the colony. Generally, colonies with more open access (e.g., ice breeding colonies or colonies with extensive sandy shores) and more uniform terrain (ice, sand) tend to have more even sex ratios, as more males are able to gain positions ashore. Rocky colonies with more restricted access and more varied terrain tend to have more female biased sex ratios. At such sites, subordinate males are less able to gain or maintain positions on the colony, hence the generally lower level of male-male aggression observed on the colony. Examples of different colony habitats can be seen in Fig. 9.6. (adapted from Twiss et al. 1998 and Bishop 2015).

### *9.3.2 Interactions Between Males and Females*

The primary interactions between males and females relate to mating. Males (tenured or transient) do not actively herd females but often ‘test’ females during lactation (Boness and James 1979, Boness et al. 1982, Anderson and Fedak 1985, Lidgard et al. 2001) by approaching them, appearing to sniff at females, and perhaps attempting to mount the female. Females in early lactation typically respond with aggressive rebuffs (Boness et al. 1982), but the intensity of this response tends to decline as females approach estrus at the end of lactation (Twiss et al. 2006). In some cases, females actively solicit males when in estrous, approaching males and rubbing their body against the male. Typically, only secure tenured males can repeatedly approach females(s) in their ‘territory’. Transient males are more opportunistic and are often very aggressively rebuffed (Boness et al. 1982, 1995). Transients, however, may attempt to force copulations (Boness et al. 1982, 1995), but often with limited success. In fact, females can express choice of mating and reproductive partner (Amos et al. 1995, 2001, Twiss et al. 2006, though also see Ambs et al. 1999), actively seeking specific males, though such behavior is often hidden as dominant, and presumably ‘desirable’ males tend to occupy territories encompassing most females’ locations anyway. Whether the initial selection of pupping sites by females is influenced by the identity or status of males already present on the colony is unknown. Females may also copulate multiple times (Anderson et al. 1975, Boness and James 1979, Twiss et al. 2006), either with the same or different males, raising the possibility, yet unproven, of post-copulatory mate choice. The duration of successful copulations is typically in excess of 20 minutes (and can extend to over 60 minutes); therefore, the probability of subordinate, transient males achieving successful copulations in the vicinity of more dominant males’ territories is small. Such mating attempts are likely to be met with both aggression from the female, and/or the local dominant, tenured male(s). Transient males are more likely to gain success in isolated or peripheral parts of colonies, where they may ‘guard’ or at least consort with individual females in an attempt to secure a mating opportunity once the female enters estrus (Ambs et al. 1999, Lidgard et al. 2001).

Compared to some other phocid species, such as elephant seals, gray seals exhibit moderate sexual size dimorphism and polygyny (González-Suárez and Cassini 2014). The extent to which specific males can monopolize mating opportunities is a key driver of the degree of polygyny observed at any colony. The ability of different male mating strategies to monopolize access to females is essentially driven by the spatial and temporal distribution of females in estrous (Twiss et al. 2007). The spatial distribution of mating opportunities is dictated primarily by the colony's physical structure and local environment (see 9.3.6). However, because males typically fast during their stay on the colony, the temporal distribution of mating opportunities is equally important to consider. The number and density of females in estrous changes during the breeding season. Therefore, males must also time their reproductive effort carefully, adaptively balancing the rewards of access to multiple females against the costs of long tenure and male-male competition (Bishop et al. 2017). However, females are not passive recipients of male attention and play an essential role in determining variation in male reproductive success. Female gray seals can react aggressively to male sexual approaches. They exhibit active mate choice, preferentially selecting the same mating partner in successive years (Amos et al. 1995), or selecting different fathers for their pups that are significantly more genetically diverse than expected from random mating (possibly via post-copulatory mate choice mechanisms, Amos et al. 2001).

While male-female interactions have been observed during the breeding season, less is known about their interactions outside the breeding season. Telemetry studies reveal some evidence of sexual differences in foraging habits and habitats (see 9.4, Chap. 6), but very little is known about inter-sexual social behavioral interactions outside of the breeding season. Information on at-sea associations may help illuminate the importance or strength of mate choice and partner fidelity during breeding.

### ***9.3.3 Interactions Between Females and Their Pups***

Interactions between mother and pup have been a primary focus of studies into gray seal behavior since early observations (e.g., Fogden 1971, Anderson et al. 1975). The mother is the sole provider for and protector of the pup during the 2–3 weeks of dependence (lactation periods tend to be shorter in the Western Atlantic populations compared to Eastern Atlantic; Lydersen and Kovacs 1999). Therefore, researchers have endeavored to understand the behavioral mechanisms involved in maternal care and the drivers of variation in the quality and success of pup rearing within and across colonies.

The immediate post-parturition period, within approximately 1 hour of birth, is a critical time for mothers and pups to establish a social bond (Davies 1949, Fogden 1971, Burton et al. 1975, Fig. 9.4), and failure to achieve this likely contributes to poor maternal care. Postpartum females bond with their pup through early behavioral interaction (Davies 1949, Fogden 1971, Burton et al. 1975), which triggers an increase in basal plasma oxytocin concentrations in the mother (Robinson et al. 2015a, 2019). These elevated plasma oxytocin concentrations likely initiate essential maternal behavior and maintenance of mother-pup proximity. Failure to achieve this early interaction interrupts the feedback between behavior and physiology, and without the elevation of oxytocin levels in the mother, appropriate maternal behavior may not be triggered. Consequently, the probability of pup mortality is much greater in the first few days postpartum (Coulson and Hickling, 1964, Burton et al. 1975, Anderson et al. 1979, Baker 1984, Baker and Baker 1988, Twiss et al. 2003). Stochastic events around the time of parturition can dramatically affect this process. For example, Robinson et al. (2015a) showed that, even in highly experienced mothers that have raised pups successfully in previous breeding seasons, disturbances during this critical time window that distract the mother from making early social interactions can disrupt the process, leading to a failure of maternal care, and likely abandonment of the pup. Distractions can include aggression from neighboring conspecifics, especially prevalent where mothers are more densely aggregated (see 9.3.6), disturbance from gulls that seek to scavenge the placenta, separation of mother and pup such as during tidal inundation on beach breeding colonies (see 9.3.6), and potential anthropogenic disturbance where humans come into close contact with seals during pupping (Burton et al. 1975). While some mothers may be more resilient to such distractions (see 9.5), the chance element means that unsuccessful pupping events can occur even among typically successful mothers. This complicates predictions of lifetime reproductive success, especially in times of rapid environmental change.

**Fig. 9.4**. Depiction of a birth sequence on the Isle of May, illustrating some of the typical challenges a mother faces immediately post-partum. Mother giving birth (a-c; time 17:14:04–17:14:32 GMT) attracts the attention of a neighboring mother (c; 17:14:32) and requires the new mother to engage in female-female aggressive interactions (d; 17:14:54). However, the new mother also needs to establish contact with the neonate, and she succeeds in making her first visual and olfactory contact despite the proximity of the neighbor (e; 17:14:56). The new mother then moves approximately 2 m further away from the neighbor, with the pup following, and positions herself to nurse the new pup (f; 17:15:22). Image credits: SD Twiss.

In addition to protecting her pup from harm, the mothers' other essential task is to provision her pup with milk (Chap. 8). Provisioning is a balance between maximizing the pup's chances of survival post-weaning (Hall et al. 2001, 2002, Bennett et al.

2007, 2010) while avoiding over-investing in the pup, which risks incurring longer-term adverse effects, such as having to skip the subsequent breeding season (Pomeroy et al. 1999). A standard component of an ethogram for mother-pup observational studies is nursing and/or presenting, where the female lies on her flank, exposing her nipples to the pup (presenting), at which point the pup typically brings its nose to the mother's nipples. The mother is often considered to be nursing when the pup makes oral contact with a nipple. It is difficult to observe when a pup is consuming milk or how much; therefore, measures of time spent in nursing and/or presenting are not well correlated with energy transfer. However, they are a measure of the behavioral effort a mother is investing in her pup and how this may change over the course of lactation. There appear to be differences across colonies in the temporal patterns of presenting and nursing. For example, Kovacs (1987) found no change in the daily proportion of time mothers at the Isle of May spent presenting and nursing as their pup grew. Yet, on North Rona, Culloch (2012) identified an increase in time devoted to presenting and nursing across lactation. At Sable Island, Lang et al. (2011) also reported that the proportion of time spent nursing increased significantly between early and late lactation. This concurs with Mellish et al.'s (1999) study, where rates of milk intake and milk fat content, which are related to pup growth rates, increased significantly during lactation, although with considerable inter-individual variation among mothers. These behavioral studies were confined to daylight observations and are not likely representative of night-time behavior (Culloch et al. 2016, Fraser et al. 2019). Using animal-mounted triaxial accelerometers, Shuert et al. (2018, 2020a.) overcame the challenges of night-time observations to identify the presenting/nursing posture during both day and night. From these studies, Shuert et al. (2020a) found that time spent presenting/nursing did not vary across lactation for 38 mothers during two consecutive breeding seasons at the Isle of May, although mothers often engaged in more presenting/nursing behavior at night than in daylight.

A theoretical expectation is that mothers, particularly those that are in better condition, should invest more in male offspring. Some studies have provided behavioral or energetic (e.g., maternal expenditure measured as the rate of mass loss) evidence of differential investment between the sexes (e.g., Kovacs and Lavigne 1986, Anderson and Fedak 1987, Kovacs 1987, Baker et al. 1995), while others have failed to find such a difference (e.g., Bowen et al. 1992, Smiseth and Lorensten 1995a, Pomeroy et al. 1999, Shuert et al. 2020a). It remains unclear whether the differences are due to local random sampling biases, or if some populations exhibit differential investment while others do not.

Despite the remaining uncertainty about whether mothers routinely differ in their behavioral and/or energetic investment in pups based on the pup's sex, individual mothers vary in attentiveness towards their pups. Some mothers regularly check on their pup, with the mother giving a definite, distinct and directed look to her pup (Twiss et al. 2012a, b, Culloch 2012, James 2013), irrespective of the pup's behavior or the behavior of conspecifics; while other mothers do so more infrequently (see 9.5). Mothers adjust attentiveness as their pup ages. On the Isle of May and North Rona colonies, Kovacs (1987) and Culloch (2012) reported that pup-checking rates decreased as the pup aged. Furthermore, on the Isle of May, young pups were accompanied by their mothers significantly more than older pups (Kovacs, 1987), suggesting that females tend to be more vigilant while the pups are most vulnerable (Anderson et al. 1979, Coulson and Hickling 1964). Mothers generally react to their pup's behavior, commonly as a result of movement or begging behavior (e.g., Fogden 1971, Kovacs 1987, Smiseth and Lorentsen 2001), although with considerable variation across mothers (James 2013).

Whether mothers or pups initiate nursing bouts has been an intriguing question that touches on parent-offspring conflict; mothers seek to provision their current pup adequately but not over-invest in any one reproductive event, while each pup seeks to maximize its gain from its mother. On the Isle of May, Kovacs (1987) reported that nursing was often preceded by the mother nosing her pup. The mother then typically presented to the pup and moved several meters, with the pup following. This was interpreted as the mother leading her pup away from conspecifics to nurse without disturbance. However, nosing behavior is performed by the pup as well, with the pup often repeatedly nosing the mother's abdominal region in an attempt to persuade the mother to adopt the presenting/nursing posture. Similar behavioral interactions between mother and pup occur on other colonies, and, in most cases, it is the pup that initiates the majority of suckling bouts (e.g., Fogden 1971, Smiseth and Lorentsen 2001, Culloch, 2012, James 2013).

Pups also produce vocalizations, which may be an essential behavioral cue for attracting maternal attention (Davies 1949, Fogden 1971). However, some observational studies have placed less weight on the importance of pup vocalizations in establishing contact when a mother comes ashore to reunite with her pup (Burton et al. 1975). A more quantitative study on these begging calls was undertaken by Smiseth and Lorentsen (2001) in the Froan archipelago, Norway, where mother-pup pairs are widely dispersed, and the mother spends considerable time in the water. There, pups begged at significantly higher rates when hungry than when satiated. Pups vocalized more often than expected by chance before their mothers came ashore and, in turn, the mothers were more likely to approach their pup shortly after it gave a begging call, indicating that mothers respond to pup vocalizations. However, it was unclear whether mothers were able to recognize and respond to the call of their pup or were simply responding to the distinctive sound of pup vocalizations in general. Caudron et al. (1998) found high levels of pup call individuality in the harmonics, but they argued that such calls were used too infrequently to play a significant role in mother-pup reunions. On the Isle of May, McCulloch et al. (1999) also found pup calls to be individually distinctive, but playback experiments revealed that mothers on this colony did not respond more to calls from their pups than to calls from non-filial pups. When conducting the same tests at Sable Island (Canada), McCulloch and Boness (2000) found that mothers responded more strongly to vocalizations from their pup compared to those of other pups, suggesting an ability to discriminate and respond preferentially to calls of their dependant pup. These studies also highlighted much higher levels of allo-suckling at the Isle of May colony compared to Sable Island. The importance of pup vocal cues with respect to ensuring a successful reunion with the mother may vary across colonies, and it remains unclear what selective pressures might enhance individual recognition capabilities in one population, or colony, compared to others.

Irrespective of stimuli that mothers respond to, mothers need to provide adequate protection for their pup throughout lactation. The majority of pup mortality during dependence results from permanent separation of mother and pup (Coulson and Hickling 1964, Burton et al. 1975, Anderson et al. 1979, Baker 1984, Baker and Baker 1988, Twiss et al. 2003). Therefore, the most critical aspect of maternal protection is to prevent the pup from straying or sustaining injuries from neighboring adults (Burton et al. 1975). Essential to such protection is the maintenance of mother-pup proximity, and recent studies have shown that proximity seeking behavior in gray seals is facilitated by elevated maternal plasma oxytocin (Robinson et al. 2015a, 2017a, 2019).

Energetic investment and protection from harm are maternal activities that all mothers engage in, but social investment in the pup is not universally essential. Maternal social investment involves affiliative physical interactions with her pup, which includes (but is not limited to) nosing (touching her pup with her nose), flippering (using her flipper to “stroke” her pup), and play behaviors. Kovacs (1987) and Culloch (2012) both found that such social interactions increased throughout lactation, which coincides with pups becoming more active and exploratory as they become older. It is not clear whether social investment has a longer-term impact upon the behavior of pups post-weaning (see 9.6). Mothers vary markedly in their tendency to perform such behaviors, with some engaging in social interactions far more than others (James 2013), which suggests distinct mothering styles. A significant challenge in furthering knowledge of the impact of such social interactions on pup development is the current inability to conduct longitudinal studies on weaned pups through to breeding age.

### *9.3.4 Interactions Between Females*

Pregnant females often lie in close proximity (even within 1–2 m) on the periphery of the colony (Pomeroy et al. 1994) and seem very tolerant of each other. However, postpartum females tend to become intolerant of conspecifics that come within 3–4 m (Boness et al. 1982, Caudron 1998, Twiss et al. 2000). Therefore, any activity that places females close to others on the colony is likely to result in an aggressive interaction (e.g., Fogden 1971, Boness et al., 1982). Reasons why mothers may come into conflict typically involve pups straying, for example, while a mother is inattentive, which often leads to aggression towards the pup from neighboring adults. Mother’s must then take remedial action to divert their pup from the potential threat or deter the neighboring adult (e.g., Fogden 1971, Boness et al. 1982, Fig. 9.5a). Conflict between females can occur as individuals commute from their pupping site to available pools of water on the colony (see 9.3.6), especially where availability of pools is limited (Fig. 9.5b), or where other environmental conditions initiate more movement, such as breeding beaches that are subject to tidal inundation (Coulson and Hickling 1964). Mothers have been reported to reduce their levels of aggression towards females in the latter stages of lactation (Boness et al. 1982), which supports the supposition that female aggression, particularly during the earlier stages of lactation when the pup is more vulnerable, is to protect the pup from conspecifics. Nonetheless, aggression between females is seldom physically damaging. Most interactions involve low-level threat behaviors such as wailing, flippering, open mouth threats, and lunging, often with erect vibrissae, ending the lunge just as the vibrissae approach or touch the opponent’s body (e.g., Fogden 1971, Boness et al. 1982, Kovacs 1987, Culloch 2012). In most cases, female-female aggressive encounters avoid biting. Even in more intense aggressive encounters, most physical contact tends to consist of aggressive flippering.

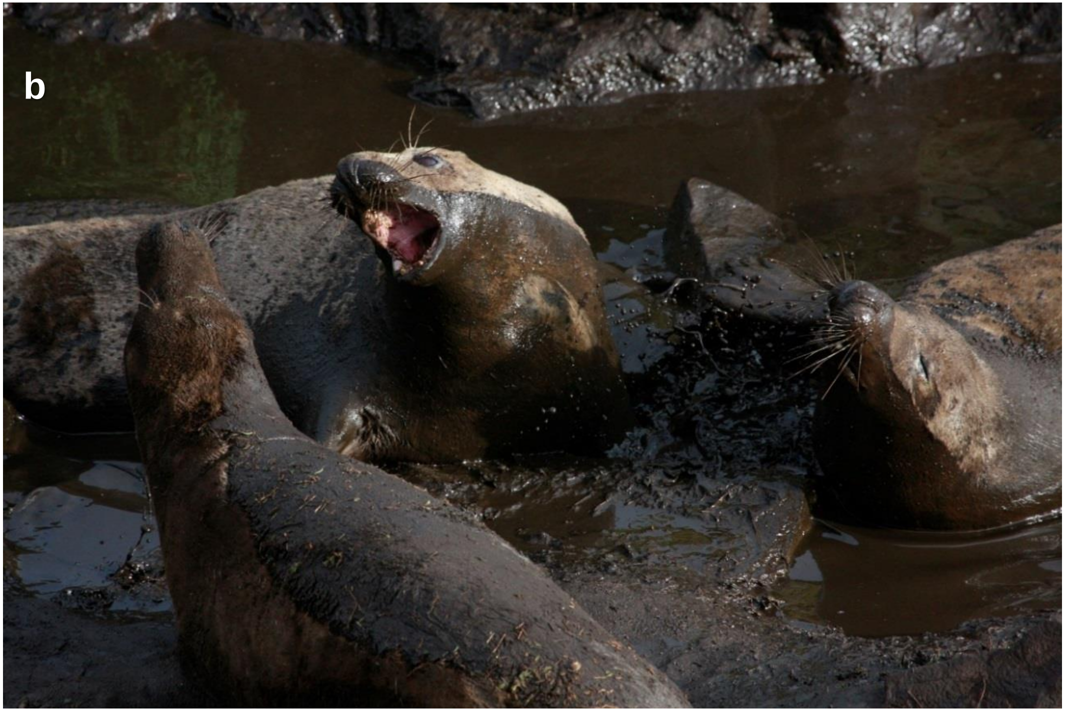


**Fig. 9.5a.** Female-female aggression on the North Rona colony in the context of protection of the pup from neighbours. The mother on the left was previously at rest, meanwhile her pup strayed too close to the neighboring mother on the right, who then lunged at the pup. This action alerted the pup’s mother who approached rapidly and can be seen exchanging open mouth threats with the neighbor, as the pup flees back to safety. We can clearly see the erect vibrissae on both mothers, and no physical contact was made between the two. Image credits: SD Twiss.

**Fig. 9.5b.** Female ‘sparring’ aggression in the context of competition over limited access to pools on the Isle of May breeding colony. All three females are mothers, who have left their pups (up to c. 50 m away in this case) to bathe and drink in this muddy wallow. All three are performing open-mouth threats, with vibrissae erect, and the right-hand female is also aggressively flippering (without contact). Such interactions tend to be less prevalent where pools are more abundant or larger, whereas they tend to increase on colonies with few, smaller, or more ephemeral pools. Image credits: SD Twiss.

One aspect of female-female social interactions that has not been adequately quantified is that of dominance relations. While quantitative measures of relative dominance among males are readily determined from observations of aggressive encounters (e.g., Twiss et al. 1998, Bishop et al. 2015b, 2017), no one has yet achieved the same for females. The problem is that female-female aggression is far more context-dependent than among males. For tenured males, the objective is to avoid being defeated by a rival and thereby losing access to potential mating opportunities (see 9.3.1). For a female, the objective is to protect her pup, and so the outcome of a female-female aggressive interaction can be determined by the actions of a third party, the pup. If the pup actively or inadvertently moves out of harm's way, then its mother often retires from a conflict with her neighbor, even though she may not necessarily be subordinate to the opponent. Therefore, simple win-loss metrics cannot be used to assess female dominance relations. In addition, an individual's willingness to engage in aggression, and the intensity of aggression, once initiated, is potentially related to behavioral type (Twiss et al. 2012, see 9.5).

Interactions among postpartum females are not solely aggressive. Often, neighboring females inspect each other non-aggressively, typically by placing their noses close together or even touching. This 'nosing' behavior (e.g., Fogden 1971, Culloch 2012) has not been examined quantitatively. Such female-female interactions may represent the behavioral process for individuals becoming familiar and/or reacquainting themselves with neighbors from previous breeding seasons. On UK breeding colonies, females can use the same breeding colony for up to 25 years (Pomeroy et al. 1999), and depending on the colony, individuals often return to within a few meters of their previous years' pupping site (median measures for levels of inter-annual site fidelity range from 25 m to 55 m, Pomeroy et al. 1994, Pomeroy et al. 2000a, Pomeroy et al. 2005). Despite this, Poland et al. (2008) found limited evidence of fine-scale kin clustering on the North Rona colony. Furthermore, neighboring mothers who were likely to interact socially because they were on the colony at the same time and in the same location, were no more related to one another than by random. Therefore, it is unlikely that the social interactions of mothers on North Rona are influenced by kin selection. However, there is evidence of non-kin based social associations occurring at North Rona. With the high degree of site-fidelity at this site, individual mothers tend to have the same neighbors over multiple years, raising the possibility of pro-social behaviors such as reduced aggression among familiar neighbors (Ruddell et al. 2007).

A likely mechanism for reduced aggression lies in the elevated oxytocin levels of mothers (see 9.3.3), a possibility highlighted by Robinson et al.’s (2015a, b, 2017a) work showing reduced levels of costly interactions among familiar weaned pups (see 9.3.5). Repeated proximity does not necessarily demonstrate active choice to be near familiar neighbors across breeding seasons and could simply be a by-product of the observed site fidelity. However, at North Rona, among females that showed less site-fidelity by pupping more than the median distance from the previous year’s pupping sites, the co-occurrence of neighbors across years was much greater than expected based on random relocations (Pomeroy et al. 2005). This indicates that at least some females formed long-term active associations and were ‘choosing’ to be near one another in successive years. At other colonies, however, such high degrees of site fidelity do not occur. Only 2.9% of females returned to their previous pupping site at Sable Island, with a median dispersal distance of 5.1 km between years (Weitzman et al. 2017). Therefore, site fidelity on Sable Island is rare; however, females spend time on the island prior to giving birth, often traveling more than 10 km over several days before deciding on a pupping site. Based on these observations, Weitzman et al. (2017) suggested that females are making decisions on their breeding site based on external cues. Of the potential mechanisms not tested in their study, they considered local density and social interactions with other gray seals as possible explanations. Since gray seals are gregarious, females may be attracted to other females as cues for appropriate breeding locations (e.g., Pomeroy et al. 2000b, 2001). Therefore, patterns of female-female interactions are likely to differ across sites dependent upon the distribution and familiarity of neighboring females.

### *9.3.5 Interactions Between Pups*

Most ethological research on gray seal pups has been of mother-pup interactions, with less on pup-pup interactions, either during the phase of maternal dependency or post-weaning. Generally, dependent pups show little motivation to interact with each other, apart from occasions when abandoned pups attempt to suckle from another pup’s mother, or follow dependent or weaned pups, again seeking (in this case, mistakenly) nursing opportunities (Smith 1968, Fogden 1971, Perry et al. 1998, McCulloch et al. 1999, McCulloch and Boness 2000). However, few quantitative studies have detailed the occurrence or consequences of these behaviors for the pup or mother.

There have been studies of interactions between weaned gray seal pups during their prolonged (up to c.40 days, Reilly 1991, Lydersen and Kovacs 1999, Bennett et al. 2007, Noren et al. 2008) post-weaning fast on the breeding colony. Building on preliminary evidence that adult females might recognize specific conspecifics (Pomeroy et al. 2005), Robinson et al. (2015b) conducted behavioral tests on wild, newly weaned gray seal pups. The authors examined investigative (olfactory or visual) and aggressive behaviors in pairs of weaners that were either strangers or had encountered each other previously. Even at the age of 3–4 weeks old, gray seal pups can recognize individuals they have previously encountered and reduce the levels of costly interactions with these familiars. Robinson et al. (2017b) went on to investigate some of the drivers of aggressive behavior between un-familiar weaned pups, showing that larger male pups tended to exhibit more aggression, while relationships between size and aggressiveness were less clear for female weaners. The social or physical environment in which a pup was raised during its dependent period strongly influenced aggressiveness, with pups that nursed in more crowded parts of the colony engaging in more aggression as weaners. These results provide evidence of possible early social environmental influences on individual behavioral profiles (see 9.5 and 9.6). Robinson et al. (2017a) also explored the role of oxytocin in behavioral expression among weaned pups by experimentally elevating plasma oxytocin concentrations. Weaned pups that received additional oxytocin tended to seek others out and remain close to one another, with reduced frequencies of aggressive and investigative behaviors. Together, these studies provide intriguing suggestions of early pro-social development in gray seals.

Although gray seals are gregarious on breeding grounds and haul-out sites, it is clear they do not exhibit high levels of sociality, with most of the interactions between conspecifics, except for mother-pup behavior, being agonistic rather than affiliative. However, they do show relatively simple pro-social behaviors, such as reduced aggression among familiars. Such behavioral mechanisms are likely to be key stepping-stones for the evolution of more complex forms of sociality (Pomeroy et al. 2005, Ruddell et al. 2007). Therefore, more in-depth studies of social interactions among individual gray seals have the potential to shed light on the early stages of social evolution.

Dependent and weaned pups engage in play and exploratory behavior (Wilson 1974, Kovacs 1987, Hunter at al. 2002), which tend to increase as dependent pups age (Kovacs 1987). However, this is typically self-directed or object play, and rarely takes the form of social play with conspecific peers (Kovacs 1987). The need to conserve energy by minimizing activity during the nursing period seems to be the main driver that constrains play behavior, at least during the earlier stages of development (Kovacs 1987). Observations of juvenile gray seals show that social play behavior occurs in the early years post-weaning (Survilienė et al. 2016). However, there has been little effort to measure this behavior, likely because juveniles are irregular attendants around the periphery of breeding colonies, making it challenging to observe. Published information on interactions between young gray seals is therefore limited and has probably been regarded as a topic of little relevance to understanding gray seal biology. However, given increasing knowledge of individual variation in behavioral strategies in adults (see 9.5), and the remarkable foraging feats of adults (see 9.4), understanding how behavior patterns develop within individuals is likely to be informative.

### *9.3.6 Interactions with the Physical Environment*

As Stirling (1975) emphasized, gray seals breed on a remarkable range of habitats, from pack ice and land-fast ice, through to sandy beaches and rugged and broken rocky terrain (Fig. 9.6). Indeed, gray seals breed over almost the entire range of habitat types utilized by all species of phocids, which has enabled detailed comparative investigations that have provided essential insights into the factors that regulate breeding patterns in phocids. Within island colonies, fine-scale spatial and temporal variations in the physical environment are fundamental drivers of individual behavior, both by the direct effects of an individual’s immediate environment, but also by the indirect effects of the environment’s impact on distribution, density, and movement of seals within colonies (Fig. 9.7). Consequently, gross differences in gray seal behaviour patterns and demographics between colonies or populations can, to a large extent, be explained by colony physical habitat (Boyd et al. 1962, Twiss et al. 2000, 2003, Matthiopoulos et al. 2005, Stephenson et al. 2007).

**Fig. 9.6.** Examples of the differing terrain across gray seal breeding colonies. Images of gray seals breeding on ice show the overall dispersion of seals (a), but also illustrate the heterogeneity of the substrate at a fine spatial scale (b). Sable Island (Canada), is a sandbar approximately 43 km long but only 1.2 km across at its widest point, providing extensive breeding grounds along its shores (c), and also in the interior of the island (d). Island colonies, such as North Rona, Scotland (e) have limited access to the sea via narrow gullies, but relatively open terrain inland for pupping, with many widely distributed pools. By contrast the Isle of May, Scotland, (f) is predominated by more irregular terrain and fewer pools. Image credits: KM Kovacs (a, b), Damian C. Lidgard (c, d), SD Twiss (e, f).

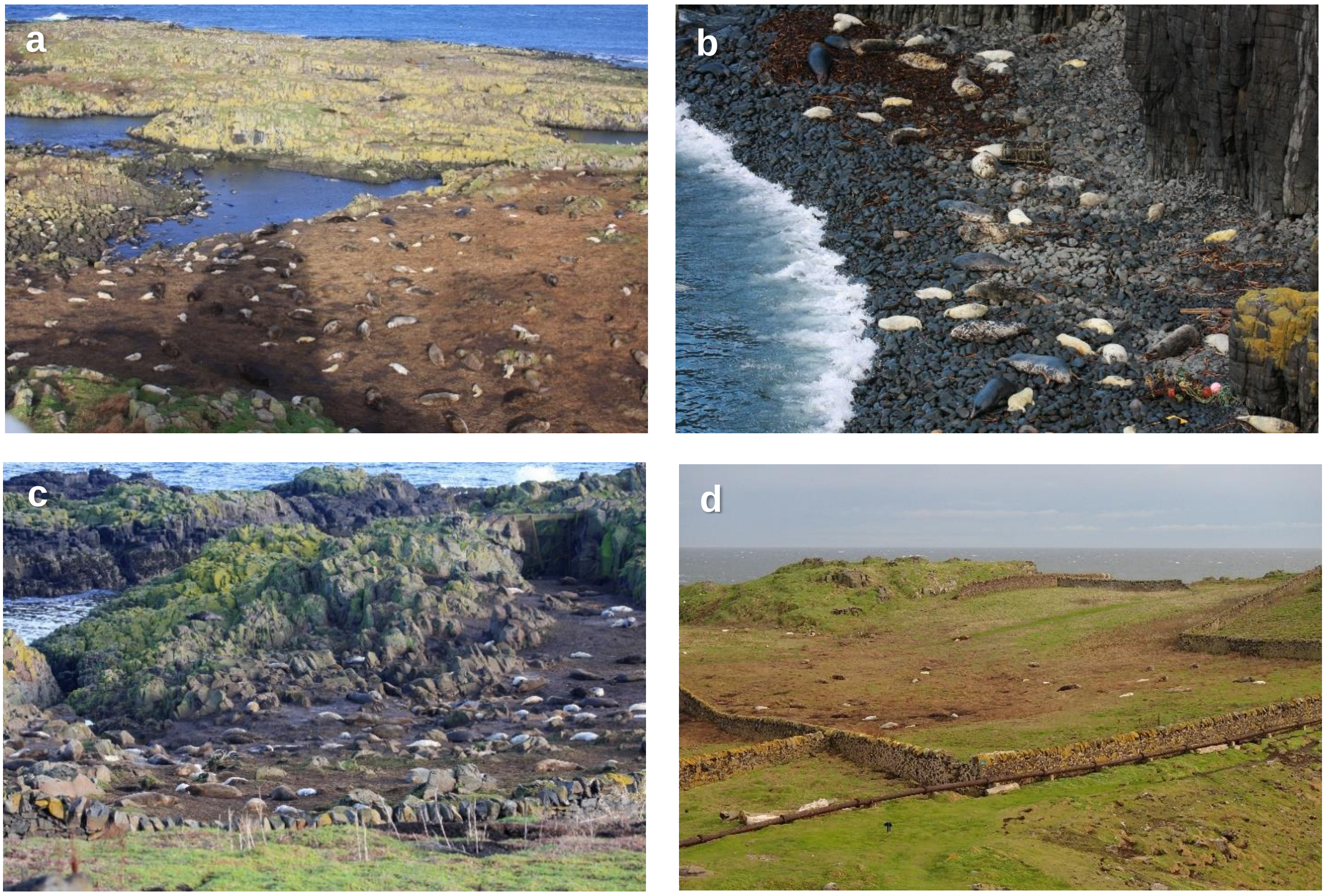


**Fig. 9.7.** Examples of the contrasting topographies and seal distribution even within one breeding colony; the Isle of May (UK). (a) Dense breeding aggregation adjacent to inlet access to/from sea. Here, mothers regularly commute between their pup on land and the large tidal inlet. (b) Tidal boulder beach, where mothers will often enter the sea, particularly during high tide. Pups tend to be pushed to the high tide line by wave action, though some pups will inadvertently be swept into the water, whilst others, particularly older pups may actively enter the water. (c) Dense breeding aggregation around limited pools in an inland site. The physical terrain dictates the availability and distribution of pools, around which pupping sites tend to cluster, and mothers will commute from nearby pupping sites to and from the pools. (d) Low density breeding area with relatively uniform terrain and no pools, and the resulting more uniform distribution of mothers and pups. There is some clustering around the damper ground (darker brown substrate), but far less than in (c). Mothers at this site rarely commute to pools (nearest is approximately 100 m away) but will do so in unusually warm conditions. These patterns of female distribution and movement, driven by the nature of the terrain, strongly influence the behavior patterns of males as they seek to monopolize mating opportunities. Image credits: SD Twiss.

The structure and stability of breeding habitat influences patterns of inter-annual site fidelity. High fidelity is often exhibited on rocky island colonies around the UK that have temporally stable intra-colony variation in pupping-site characteristics and quality (Pomeroy et al. 1994, Twiss et al. 1994, Pomeroy et al. 2000a). Conversely, site fidelity is limited on more uniform or unstable or unpredictable substrates such as land-fast or pack ice (e.g., Lydersen et al. 1994, Haller et al. 1996), or the shifting sand of Sable Island (Weitzman et al. 2017).

Given the restricted movements of mothers during lactation, fine-scale habitat quality of pupping sites influences time-activity budgets of lactating females (Anderson and Harwood 1985, Twiss et al. 2000, Shuert et al. 2020a) and the level and quality of pup attendance (Twiss et al. 2000, Redman et al. 2001, Pomeroy et al. 2001), with probable consequences for female energetics (Shuert et al. 2020b and pup survival (Boyd et al. 1962, Summers et al. 1975, Twiss et al. 2003). Breeding substrate also strongly influences behavioral patterns during the breeding season. Although most studies show a high proportion of time-activity budgets spent in rest (typically over 60%) by adult males, females and pups (e.g., Anderson and Harwood 1985, Kovacs 1987, Haller et al. 1996, Twiss et al. 2000, Bishop et al. 2015c, Fraser et al. 2019, Shuert et al. 2020a), the levels of activity are driven in part by accessibility to the sea. Lactating mothers breeding on the periphery of land-fast or pack ice or tidal beaches or inlets tend to spend more time in the sea (Fig. 9.7), though still retaining proximity to their pups, who generally remain on the ice or shoreline (Cameron 1967, 1969, Anderson and Harwood 1985, Kovacs 1987, Lydersen et al. 1994, Haller et al. 1996, Twiss et al. 2000, 2001). Seals that are subject to tidal inundation spend more time in the sea (Anderson and Harwood 1985, Smiseth and Lorentsen 1995b, 2001, Twiss et al. 2000) and experience greater disruption, periodically separating mothers and pups, rearranging neighbors, and disrupting social organization (Bishop et al. 2015b). When adult seals enter the sea during the breeding period, there is the potential for both males and females to supplement their energy reserves by feeding (Lydersen et al. 1994, Lidgard et al. 2003). By contrast, when seals remain on land throughout the breeding period, they must sustain their activity, and for mothers, the provisioning of their offspring, exclusively on energy reserves acquired prior to the breeding period (Chapt. 8). Unlike many breeding pinnipeds (especially among otariids but also elephant seals), gray seal mothers tend to maintain a ‘personal’ space between themselves and their neighbors of at least 1–2 adult body lengths, even among the densest aggregations (Boness et al. 1982, Twiss et al. 2000), allowing them to protect their pups from neighbors. However, distributions of mothers on colonies are still patchy, with varying densities and degrees of aggregation dependent upon topography (e.g., Anderson and Harwood 1985, Twiss et al. 2000, 2001, Fig. 9.7). In more uniform terrain, such as sandy beaches, mothers are more evenly distributed, whereas in more irregular terrain densities and aggregation sizes vary.

Gray seal mothers prefer to pup close to water for thermoregulation (Redman et al. 2001, Twiss et al. 2002) and drinking (Stewart et al. 2014), and the distribution of pools of fresh, brackish, or seawater consequently drives much of female spatial distribution. The location and temporal permanence of pools is a product of local topography, substrate permeability, and prevailing weather conditions. Not all females are able to gain pupping sites close to pools and may have to periodically commute to pools, especially in drier, warmer conditions (Redman et al. 2001, Shuert et al. 2020a,b). Such commuting comes with associated risks of permanent separation from offspring, as pups do not commute but may wander from their pupping site while the mother is away (Redman et al. 2001), and mother-pup separation is a significant cause of pup mortality (Summers et al. 1975, Anderson et al. 1979, Baker 1984, Baker and Baker 1988, Twiss et al. 2003). Therefore, the availability and distribution of pools relative to pupping sites strongly influence maternal behavior and, consequently, pup behavior. Where pools are few, small, or aggregated in distribution, access to pools may also be dependent upon maternal dominance, with potentially more dominant or experienced females gaining pupping sites close to pools (Twiss et al. 2000, Pomeroy et al. 2001). However, occupying such sites during pup rearing also incurs costs, due to higher densities of seals and regular disruption from incoming commuters (Redman et al. 2001, Stephenson et al. 2007, Fig. 9.5b). At colonies with limited or no pools, such as Sable Island, females tend to remain with their pups throughout lactation (Perry et al. 1998, McCulloch and Boness 2000), presumably deriving all water needs from fat metabolism (although seals have been observed eating snow at this site, Twiss pers. obs.). What impact no access to drinking water has on the reproductive physiology of gray seal mothers is unknown. However, with the breeding season spanning mid-winter, with much lower ambient temperatures, seals at Sable Island may be less thermally stressed than those occupying inland pupping sites at UK colonies in the autumn.

The spatial distribution and behavior of males on the breeding colony are driven indirectly by topography because males compete for access to aggregations of females (Boness and James 1979, Anderson and Fedak 1985, Twiss et al. 1994, 2007, Tinker et al. 1995, Haller et al. 1996, Lidgard et al. 2003, Bishop et al. 2017, see 9.3.1 and 9.3.2), and female aggregations are primarily determined by topography. More dominant males can maintain ‘prime’ positions among the larger or denser aggregations of females, typically located close to larger, more permanent pools. As the distribution and availability of water and prevailing ambient temperatures influence the degree of commuting of mothers, this inevitably impacts male behavior. Increased female mobility leads to reduced potential for dominant males to monopolize access to females, consequently reducing the degree of polygyny and intensity of sexual selection (Twiss et al. 2007). Notably, this link between topography (pools), ambient temperatures, female distribution, and behavior is a critical consideration in the context of environmental change. More unpredictable weather conditions during the annual gray seal breeding season, with exposure to drier, warmer conditions are likely to lead to more females commuting, potentially more mother-pup separations, more pup abandonment, and changes in the mating pattern (Twiss et al. 2007, Shuert et al. 2020b). This link between topography and weather patterns is a crucial driver of both female and male reproductive success across all gray seal breeding habitats, and understanding the effects of climate change on these processes is essential for predicting future impacts on population dynamics (Jussi et al. 2008, Kovacs and Lydersen 2008, Kilmova et al. 2014).

## 9.4 Interactions at sea.

It is challenging to reduce knowledge gaps of at-sea behavior, particularly for long-lived, far-ranging species such as gray seals. At the surface, visual observations of behavior inevitably lack context, as most of an animal’s time is spent below the surface. The development of biologging technology in the 1970s and 1980s provided new tools for investigating the at-sea behavior of marine mammals (Chaps. 5 and 6).

Along with Weddell (*Leptonychotes weddellii*, Chap. 13) and elephant seals (Mirounga spp, Chap. 11 and 12), gray seals were the subjects of some of the first deployments of VHF and satellite telemetry devices. The first insights into movements and foraging strategies of gray seals at sea were published in the early 1990s (Thompson et al. 1991, McConnell et al. 1992). Building on this initial work, researchers have generated some of the most extensive, most detailed, and informative datasets of phocid behavior at-sea using the gray seal study system. There have been numerous publications using telemetry data to investigate gray seal movement patterns (Thompson et al. 1996, McConnell et al. 1999), foraging areas (Jessopp et al. 2013, Gosch et al. 2019), seasonal variation in foraging (Breed et al. 2009, Chap. 6), sexual segregation (Beck et al. 2003, Carter et al. 2017) and the potential impacts of anthropogenic disturbance on behavior (Mikkelsen et al. 2019).

Extrinsic and intrinsic factors inevitably drive at-sea behavior. For example, Carter et al. (2017) found that water depth contributed significantly towards sex differences in diving behaviors. Females foraged in shallower waters than males but spent more time closer to the seabed. Sex-specific reproductive requirements could drive seasonal variation, both broadly across the species and between sexes (e.g., Austin et al. 2004, Breed et al. 2013, Carter et al. 2017), a supposition supported by studies on gray seal diet composition (e.g., Beck et al. 2003, Beck et al. 2007). In adult gray seals, differences in fatty acid signatures were greatest between adult males and adult females during the post-breeding period. During this time, females foraged more selectively on higher quality prey than males, likely due to females needing to recover energy supplies to support pregnancy (Beck et al. 2003, Beck et al. 2007). While the interpretation of telemetry data can be challenging, the above examples highlight how complementary studies such as fatty acid analyzes can provide additional information to enhance behavioral inferences from telemetry deployments.

Telemetry devices can help ascertain time-activity budgets for gray seals by using metrics that are more spatial than behavioral, such as the percentage of time spent at given distances to shore (e.g., Breed et al. 2013). Time-activity budgets can also be derived from both location and movement data (e.g., McClintock et al. 2013, Russell et al. 2015, Mikkelsen et al. 2019). Russell et al. (2015) investigated population-level time-activity budgets using telemetry data from 63 gray seals, defining four behavioral states comprising resting at sea, resting on land, and two components of diving, traveling and foraging. Both juveniles and adults exhibited sex-specific seasonal variation in the proportion of time spent foraging and traveling. However, there was no evidence of sex, age, or seasonal trends in time spent in the broader behavioral categorizations of resting (on land and at sea) or diving (combining both traveling and foraging). The authors hypothesized that gray seals may exhibit little flexibility in the proportion of time spent resting, suggesting possible constraints on the levels of activity at sea. Alternatively, the seals may be able to vary the allocation of resting or diving into their respective parts (i.e., resting on land, resting at sea, traveling and foraging) in response to varying intrinsic and extrinsic drivers to obtain their energetic requirements. Studies such as these illustrate how telemetry data can provide time-activity budgets for seals at sea and how that time partitioning varies across individuals.

The focus of recent telemetry studies has often been driven by management or conservation concerns, particularly in the context of interactions with, or consequences of, anthropogenic activities in the marine environment. However, such studies still yield important behavioral insights. One area to receive substantial attention is interactions with commercial fisheries (e.g., Cronin et al. 2016, Jessopp et al. 2013, Königson et al. 2013, Stavenow et al. 2016, Vincent et al. 2016). In many areas where gray seals and fisheries co-exist, there is often a management need to assess overlap and interaction (e.g., Jessopp et al. 2013, Stavenow et al. 2016). In the Baltic sea, evidence from underwater cameras showed that some adult male gray seals have exploited a niche to become specialized in raiding salmon traps (Königson et al. 2013). Observations of 600 seal visits to two salmon traps revealed that 426 were made by just 11 individuals, four of whom regularly returned throughout the two-year study. The authors concluded that these seals had developed a characteristic behavior pattern that has persisted over a long time.

In Irish waters, Cronin et al. (2016) provided evidence that gray seal space use overlapped with passive fishery locations (i.e., fisheries using static gear such as tangle, trammel, and gillnetters) much more than with active gear fisheries, such as trawls. The authors suggest that physical interactions at the net may be by a small number of individuals that have learned net-feeding behavior, reinforced with the reward of an ‘easy meal’ that requires minimal energy to acquire. In the Baltic Sea, van Beest et al. (2019) found that adult male and female gray seals favored areas with similar physical and environmental features as active fisheries. However, they stressed that overlap with fisheries was minimal (where the seal was <5 km from an active fishing net occurred ca. 3% of the time), indicating that the temporal aspect is critical for inference when investigating seal interactions with fisheries using telemetry data. Such studies provide valuable information that can improve our understanding of habitat use and potentially contentious issues, such as resource overlap and competition between top predators and fisheries, essential for the effective conservation and management of charismatic, top marine predators. These studies also give insight into how behaviorally adaptable gray seals might be (see 9.5 and 9.6), and their potential to cope with rapid changes to their environment (e.g., Russell et al. 2014).

Telemetry studies of gray seals at sea often identify a considerable degree of individual variation in behavioral patterns and, in many cases, individuals show clear preferences for foraging sites and routes to and from haul-out sites (e.g., McConnell et al. 1992, 1999, Austin et al. 2004, Breed et al. 2013, Jessopp et al. 2013, Russell et al. 2015, Lidgard et al. 2020). Whether these patterns are indicative of specific behavioral types or not (see 9.5) is unclear, but it indicates some degree of individual behavioral specialization. Often, our understanding of at sea behavior is limited to small sample sizes, particularly in cases where expensive telemetry devices are used. Deliberate repeat tagging of individuals is rarely undertaken to avoid pseudoreplication. However, there is value in understanding how individuals use their habitat across years, as this can provide insights into the development of foraging strategies and preferences and the extent of behavioral plasticity that gray seals might exhibit, all of which are key considerations in a rapidly changing environment. The telemetry studies cited in this section, among many others, have provided valuable insights into at sea behavior (Fig. 9.8) and have ultimately helped us to better understand how seals use their marine and terrestrial habitats. There remains a paucity of information on how individuals interact with one another while at sea, primarily due to a current lack of technological solutions (Baker et al. 2014).

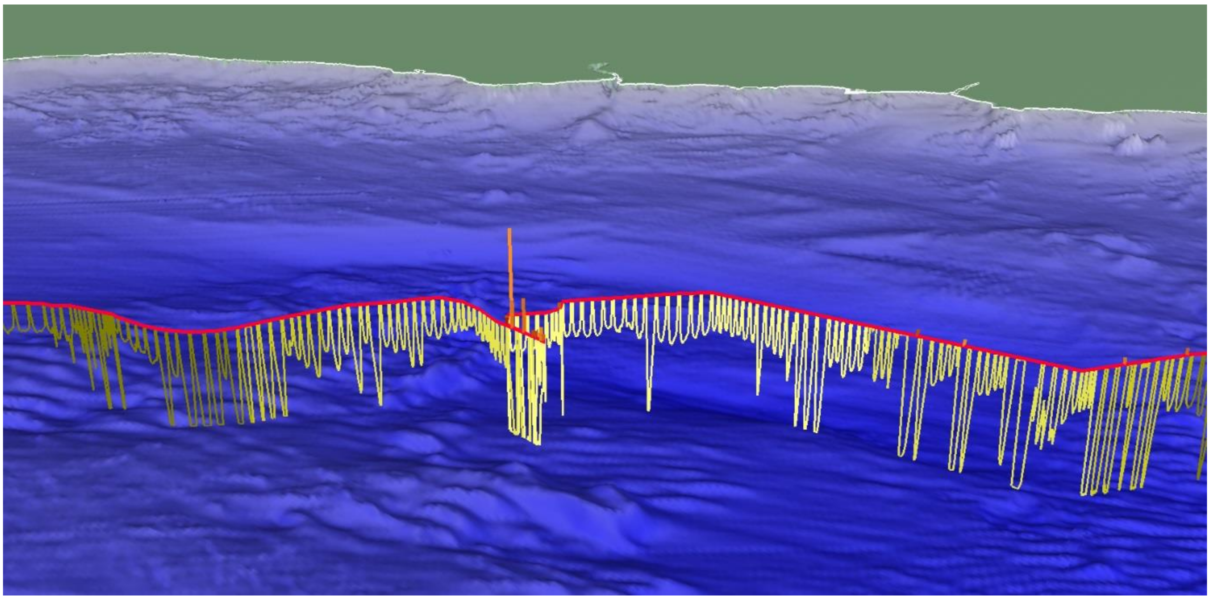


**Fig. 9.8.** A 3D track of a grey seal at sea (in  North Sea, UK), showing not only location and depth but also behavioral events. On-board processing of accelerometer data from a GPS phone tag detects possible prey capture attempts. The vertical orange bars indicate the number of prey capture attempts in each successive phase of diving (descent, bottom and ascent). Telemetry devices were deployed by Cecile Vincent (CNRS/ Uni. De la Rochelle), image created by Sea Mammal Research Unit using MamVisAD. Bathymetry source: EMODnet 2018 DTM.

## 9.5 Personality

Despite the general patterns in behavior in relation to the breeding environment, there remains considerable individual variation in behavior at all colony habitat types (Lydersen and Kovacs 1999, Twiss et al. 2000). This individual variation is driven in part by the local habitat and environment (e.g., Lydersen et al. 1994, Tinker et al. 1995, Twiss et al. 2000, 2001, 2007, Redman et al. 2001, Stewart et al. 2014), but other factors play important roles, including individual age and experience (Godsell 1991, Haller at al. 1996, Lidgard et al. 2012), status (Boness and James 1979, Twiss et al. 1998, Bishop et al. 2015b), and condition (Anderson and Fedak 1985, Tinker et al. 1995, Mellish et al. 1999, Pomeroy et al. 1999, Lang et al. 2009). However, even among individuals of the same age, sex, and status, we still observe apparent individual differences in behavior, a level of individual variation akin to personalities.

The concept of personality in non-human animals in ethological research has seen a remarkable growth of interest over the past two decades, with much debate over what constitutes personality in non-human animals. A review of that debate is beyond the scope of this chapter, but a useful introduction to the topic can be found in Briffa and Weiss (2010), with more detailed discussions in Sih et al. (2004), Réale et al. (2007), Dingemanse et al. (2010), and Carere and Maestripieri (2013). At its heart is the concept that individuals, even within the same age and sex class, differ in their behavior and do so consistently over time, functional contexts (such as foraging or courtship), and/or situations (differing local environmental conditions). Although this does not preclude the possibility of behavioral flexibility (plasticity) in individuals, it does mean that individuals tend to maintain consistent rank order differences in behavioral expression, even if that behavioral expression is modified in response to internal or external stimuli. Evidence of such consistent individual differences (CIDs) in behavior has been revealed in a remarkably wide range of taxa, from Cnidaria (Briffa and Greenaway 2011) to Mammalia (Bell et al. 2009, Smith and Blumstein 2008), suggesting that such within-population variation is a fundamental evolutionary condition under strong or persistent selective pressure, or is a product of constraints on developmental plasticity that are widespread (Duckworth 2010). Either way, understanding the causes and consequences of inter-individual variation is critical for our comprehension of how organisms respond to their environment (Sih et al. 2012, Wolf and Weissing 2012, Dochtermann and Dingemanse 2013). There are still few studies of personality differences in marine mammals (Highfill and Kuczaj 2007, Twiss et al. 2012, 2020, de Vere et al. 2017, Frick et al. 2017, DeRango et al. 2019), with the only definitive studies of CIDs in phocids being on gray seals during the breeding season.

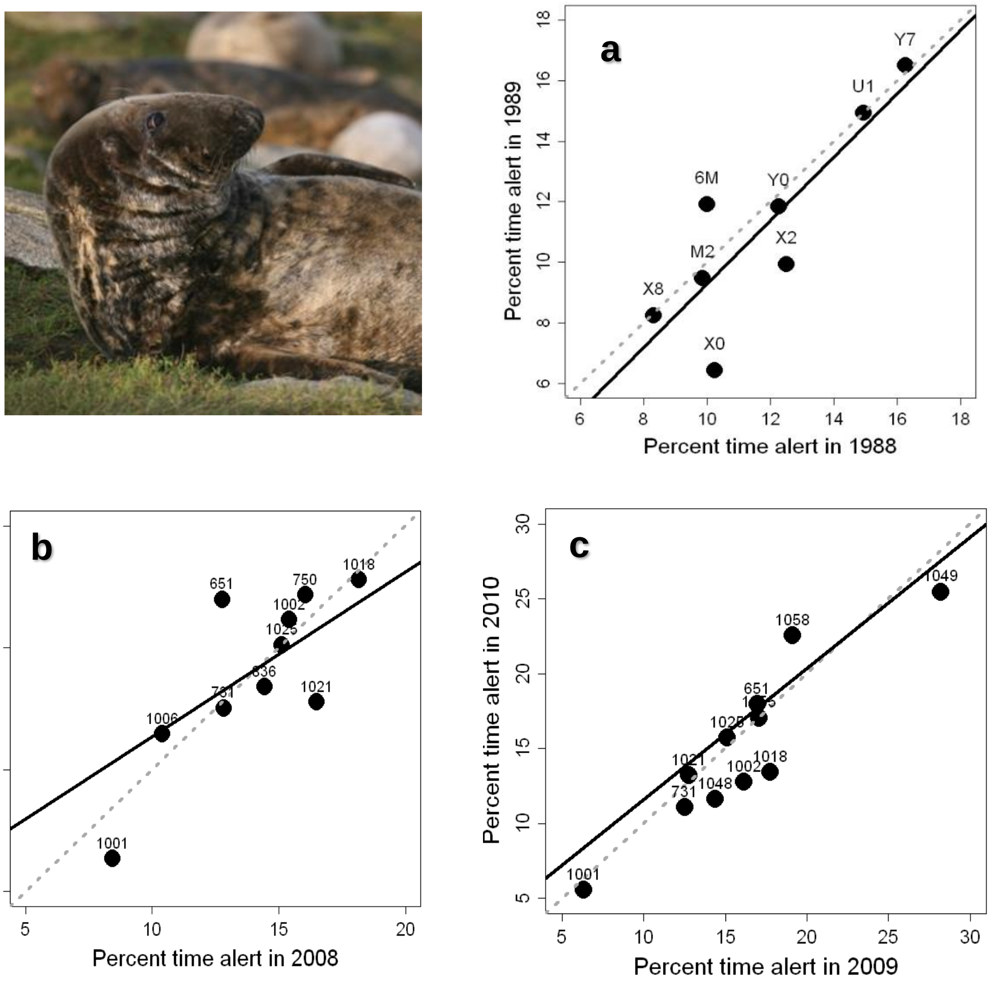
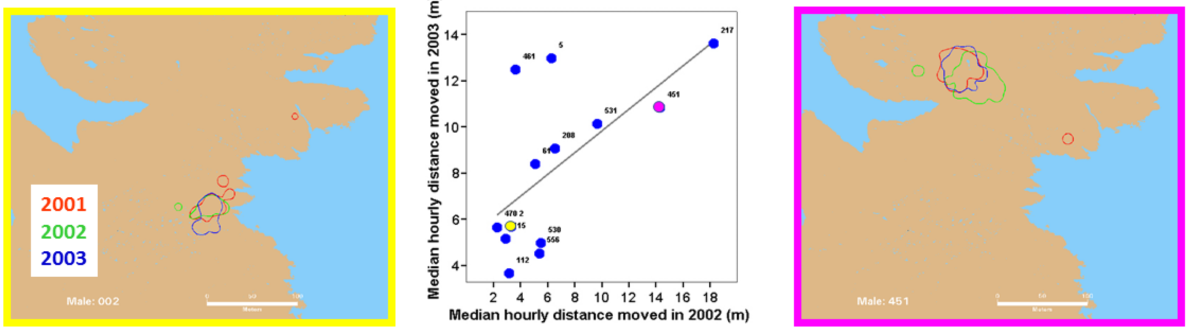
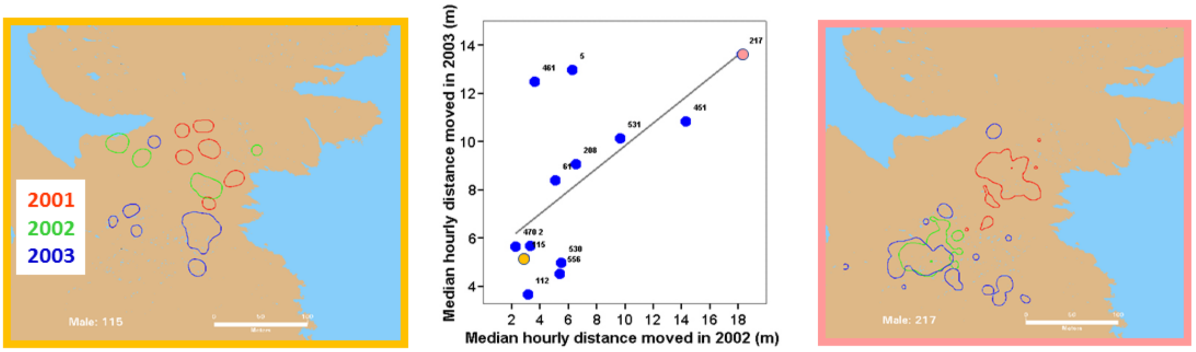


**Fig. 9.9.** Consistent individual differences in male gray seal behavior across multiple breeding seasons at the North Rona colony. Tenured males exhibited interannual consistency in time spent alert across consecutive seasons (a-c), in 1988 and 1989 (Twiss and Franklin 2010), but also among males present in 2008, 2009, 2010 (Twiss; unpublished). Repeatability was highly significant in all plots (**1988/89**: ICC = 0.83, $F_{7,7} = 10.9$, p = 0.002, **2008/09**: ICC = 0.79, $F_{9,9} = 8.3$, p = 0.002, **2009/10**: ICC = 0.91, $F_{10,10} = 21.0$, p < 0.0001). These individually differing tendencies to perform vigilance behaviors were not related to levels of external stimuli but appear to be inherent differences among individuals that are consistent over time. None of the males present in 1988/1999 were present in 2008-2010, and yet the same pattern of consistent individual differences exists across these different generations of males. In all plots the solid line represents linear regression, and dashed line indicates the 1:1. Alphanumeric codes represent male identities. Image credits: SD Twiss.



**a: High site and movement fidelity across years**



**b: Similar movement patterns but no site fidelity across years**

**Fig. 9.10:** Examples of interannual behavioral consistency in terms of space use on the breeding colony by tenured males on North Rona, showing consistent movement patterns and high (a) or low site fidelity (b) (Twiss; unpublished). Space use metrics were derived from a sub-metre accurate GIS of male locations during the 2001-2003 breeding seasons. The scatterplots depict the median hourly distances moved by tenured males within their territories for males present in 2002 and 2003 (similar patterns exist when comparing 2001 and 2002). Individual movement patterns remained consistent across successive breeding seasons (**2001-2002**: r=0.81, p<0.001, **2002-2003**: r=0.79, p=0.001). Such consistency might be explained by male site fidelity (Twiss et al. 1994), such that individuals that occupy similar locations in each year are therefore exposed to similar levels of stimuli, but that explanation does not apply to all males. The maps depict the territories (95% kernel density estimates) of two site faithful (a) and two unfaithful (b) males across 2001-2003 and highlights their movement metrics on the scatterplots with points to match the colored borders around their respective maps.

As far back as 1949, Davies observed that gray seal pups had different ‘personalities’, while in 1994, Lydersen et al. commented on the distinct differences in “manner” and “character” of mothers. Twiss and Franklin (2010) were the first to quantitatively show CIDs in behavior by examining vigilance patterns in adult males across successive breeding seasons (Figs. 9.9 and 9.10). Subsequent studies confirmed that vigilance behaviors provide useful metrics of individual differences in behavioral types for breeding females as well (Twiss et al. 2012). For example, postpartum gray seals exhibit individually different rates of pup-checking behavior that remain consistent both within and across breeding seasons. This seems to be a general pattern as it has been observed on multiple UK breeding colonies (Twiss et al. 2012, Culloch 2012, James 2013). These measures of CIDs in vigilance behavior were all derived from observational studies of wild gray seals. Twiss et al. (2012), however, used a remotely controlled vehicle to experimentally manipulate the exposure of wild breeding seals to a novel auditory stimulus. Again, CIDs in pup checking behavior were observed, but the degree to which individual mothers altered their pup-checking behavior from undisturbed (natural) to disturbed (remote-controlled vehicle) situations varied. Some mothers maintained consistent pup-checking rates across the two situations, while others raised pup-check rates in response to the novel stimulus. Twiss et al. (2012) argued that these individual differences in behavioral plasticity likely reflect pro- and reactive stress-coping styles that have a known physiological basis that drives the observed behavioral differences (Koolhaas et al. 1999, Biro and Stamps 2010, Carere et al. 2010, Coppens et al. 2010, Twiss et al. 2020., Fig. 9.11). Twiss et al. (2020) and Shuert et al. (2020a) used an integrative physiological indicator of stress-coping style (resting heart rate variability) in free-ranging gray seals to show that individual coping styles can influence both behaviour and success during the breeding season. Shuert et al. (2020a) show that stress-coping styles influence time-activity budgets, especially the trade-off between time spent in rest (conserving energy) and time spent being vigilant (monitoring their local environment and/or reacting to stimuli), with with more proactive mothers tending to spend relatively more time vigilant. Twiss et al. (2020) provided evidence that stress-coping style influences short term (within season) reproductive performance, with the behaviorally flexible reactive mothers exhibiting more variation in reproductive expenditure and consequent pup growth rates than proactive mothers.

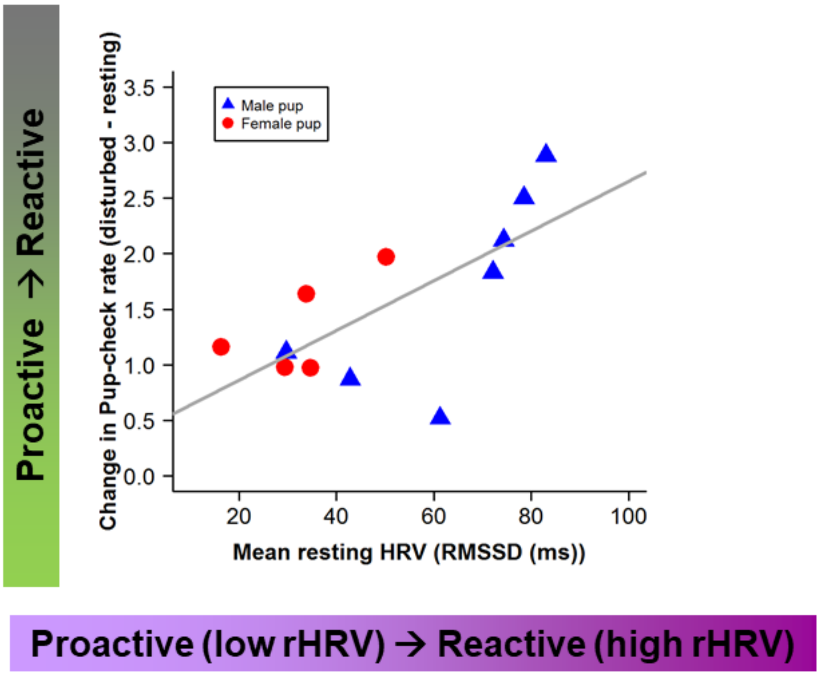


**Fig. 9.11.** The relationship between physiological indicators of stress-coping style and observational measures of behavioral plasticity among lactating females on the Isle of May in 2014 ($r_s = 0.59$, $n = 12$, $p = 0.021$; Twiss, unpublished). Coping-style is measured by the integrative physiological parameter of resting heart-rate variability (rHRV); low rHRV indicates proactive individuals, high rHRV indicates reactive individuals (Koolhaas et al. 1999, Twiss et al. 2020). Behavioral flexibility in this case is based on how much individuals change their pup-checking rates from undisturbed situations to a disturbed situation (tested used a standardized stimulus delivered by remote controlled vehicle, Twiss et al. 2012b). These data show that behavioral flexibility is linked to underlying physiological traits that dictate how individuals react to stimuli.

Even within the wider personality literature, few studies examine the longer-term persistence of CIDs in long-lived species, especially in wild populations (Trillmich et al. 2018). Bubac et al. (2018) recorded behavioral responses of over 400 gray seal mothers to human approach and the handling of their pup, providing repeated scores of individual boldness (response to a potentially risky situation, Réale et al. 2007) over nine successive breeding seasons on Sable Island. This extensive study demonstrated individual differences in boldness that were highly repeatable between and within years. Younger females tended to be less bold than older, more experienced mothers, which the authors argue may represent a life-history trade-off where younger mothers, with higher future reproductive potential, are more risk-averse.

Among the published literature, there is tantalizing evidence of individuality in many aspects of gray seal behavior. During the breeding season, females and males show high levels of site fidelity (Pomeroy et al. 1994, Twiss et al. 1994, though see Weitzman et al. 2017), males exhibit consistency of duration of tenure (Lidgard et al. 2012), and mothers show repeatable individual differences in their physiological capacity to provision their pups with milk (Lang et al. 2009). Outside of the breeding season, gray seals exhibit considerable variation in foraging behavior and at sea movements (McConnell et al. 1999, Austin et al. 2004, Lidgard et al. 2020), including evidence of foraging specializations (Tucker et al. 2007). One difficulty with at sea behavior is that few tracking studies followed the same individuals over multiple deployments of devices, and so longer-term persistence of individual differences in at-sea behavior has not been verified.

What is clear from this work is that a seal is not just a seal; there is a spectrum of behavioral types and life-history strategies within populations. This realization is essential when considering intra- and interspecific interactions and for refining models of potential population responses to environmental change. The existence of CIDs implies constrained behavioral plasticity within individuals and/or differential plasticity across individuals. Therefore, environmental changes are likely to impact specific sub-sections of the population more than others (Sih et al. 2012, Wolf and Weissing 2012).

## 9.6 Ontogeny of Behavior

There are few published studies of behavioral development in young gray seals beyond the interaction between the pup and mother (see 9.3.3). During the nursing period, gray seal pups spend most time resting (Kovacs 1987). Reduced activity is likely strongly selected to conserve energy, thereby maximizing growth and the deposition of energy-rich blubber (Lydersen et al. 1995, Lydersen and Kovacs 1999), as mass at weaning is a significant determinant of first-year survival (Hall et al. 2001, 2002). Once weaned, gray seals often remain on the breeding colony for several weeks, and interactions among weaned pups can influence behavior patterns, along with the earlier social environment during pup dependence (Robinson et al. 2015a, b, 2017a, b). However, it remains unknown whether these are persistent changes that influence life-long behavior patterns of individuals. What determines the length of the post-weaning fast is unclear; there are physiological limits to the post-weaning fast (Bennett et al. 2010, Chapt 4 and 8), but local topography and particularly the availability of larger pools of water likely influence the length of stay on a colony and whether weaners gain much experience of the aquatic environment before venturing out to sea (Kovacs 1987). Ease of access to the sea from the colony also plays a role in at least providing an opportunity for early departure, and potentially earlier development of foraging skills (Smiseth and Lorentsen 1995b, Jenssen et al. 2010).

Less is known about how behavior patterns develop once young seals leave the colony. This is a critical phase for young, naïve gray seals that must learn to dive and hunt effectively, if not entirely efficiently, before their blubber and protein reserves become depleted (Bennett et al. 2010). This learning seems to be mostly independent, as there is no evidence of a maternal role post-weaning. Analysis of location and dive data from animal-borne telemetry devices deployed on weaned gray seal pups as they depart their natal colonies for the first time provide some insights into the development of dive characteristics (Bennett et al. 2010, Carter et al. 2017). During their first 40 days at sea, gray seals show rapid increases in dive duration, depth, bottom time, and benthic diving. However, Carter et al. (2017) also found sex and regional differences in diving behavior development, suggesting that both intrinsic and extrinsic factors, such as water depth, contribute to early sex differences in foraging behavior (see 9.4). Sex differences in foraging are also apparent in the latter stages of the first year of life, which is particularly interesting as size dimorphism is not fully developed at this stage of life (Breed et al. 2011, Russell et al. 2015).

Breed et al. (2011) compared the diving behavior of young-of-the-year (5 to c.15 months of age) to the behavior of sub-adult and adult gray seals in the northwest Atlantic. The telemetry tracks of these seals suggested that young-of-the-year navigated with similar capabilities to older individuals but tended to undertake (or be forced into) longer foraging trips that were further from their haul-out sites. Unlike adults, which also have the demands of the annual breeding season to modify foraging patterns, young-of-the-year responded primarily to seasonal patterns of prey availability and condition. The development of foraging capacity is strongly tied to the development of physiology during these early phases of life (Chapt 4). Although the post-weaning fast is critical in developing the physiological capacity to commence diving behaviors, weaned pups are still developing physiologically as they depart their natal colonies (Noren et al. 2008, Bennett et al. 2010).

While biotelemetry studies can provide insights into changing dive capabilities of individuals, they, unfortunately, reveal little about the actual learning processes involved. However, experiential learning is probably fundamental to young seals continuing to refine their foraging capabilities during their first few years at sea. Whether seals learn from observing conspecifics is unknown. Observations of play in juveniles (Wilson 1974, Survilienė et al. 2016) provides some indication of mechanisms of behavioral or at least social development, but such studies are few and limited in scope. The primary logistical challenge is following specific individuals from weaning through to reproductive age and measuring not just the physical environment and food availability they encounter, but also their social environment during juvenile and sub-adult phases. These early years of independence are likely especially formative and potentially vital in determining individual behavioral profiles (Trillmich et al. 2018), and consequently, individual life history trajectories (such as pro- vs. reactive behavioral types, see 9.5), but they remain a major gap in our knowledge.

Behavioral traits are often labile and have the potential for modification throughout an individual’s lifespan. As by-products of studies with other research foci, there have been some intriguing indications of learning capacity and cognitive capabilities in gray seals, but no direct investigations of these faculties. Oliver (1977) investigated the ability of a captive juvenile male gray seal to navigate a maze. Although the focus of this study was on the sensory modalities used in detecting the presence of objects underwater in light and dark conditions, the study indicated some spatial learning and memory capacity evidenced through reduced error rates over repeat trials. Götz and Janik (2010, 2011) demonstrated both sensitization and habituation of gray seals to anthropogenic sounds with studies aimed at investigating the behavioral response to aversive sound signals (such as ‘seal scarers’) in water (Chapt 2).

Interestingly, these studies demonstrated long term behavioral changes in (avoidance) behavior in both captive and wild settings. Stansbury et al. (2015a) show that juvenile gray seals can learn to use sounds from acoustic fish tags to indicate the location of a food reward, demonstrating that gray seals have the capacity for associative learning of novel cues. Further evidence of cognitive capabilities, at least in response to auditory stimuli, comes from studies investigating gray seal ability to identify and classify call types (Shapiro et al. 2004), and to generalize acoustically similar calls into classes (Stansbury et al. 2015b). Although it remains unknown how seals might discriminate different call types in terms of the auditory information the seal is accessing, such studies raise the possibility that gray seals may be able to distinguish between calls of different conspecifics. This is particularly intriguing given the evidence of social associations in this species (Pomeroy et al. 2005, Ruddell et al. 2007). Evidence of continued ability to learn in adulthood comes from Königson et al.'s (2013) study showing that adult males can alter their foraging behavior and adopt new foraging skills (targeting salmon traps, see 9.4). Russell et al. (2014) showed intriguing evidence of gray seals' abilities to adapt their foraging behavior to exploit novel opportunities provided by anthropogenic underwater structures (e.g., pipelines, wind turbine bases). Other 'new' behaviors observed among gray seal populations may further support this ability of individuals to modify their behavior patterns throughout life (see 9.7), though the degree of behavioral plasticity may vary across behavioral types (Twiss et al. 2012, 2020, see 9.5). Studies of learning and cognition in gray seals remain scarce and are understandably based on a few individuals. However, given the evidence of considerable individual variation in a wide range of behaviors and behavioral types in this species, much remains to be discovered about the learning capacity of gray seals of all ages and behavioral types.

## 9.7 Novel Observations and Emergent Behaviors

Despite the long history of gray seal behavioral studies, researchers still find new behaviors, either unobserved previously or newly evolved. While the general gray seal behavioral repertoire is conserved across colonies (Hewer 1957, Boness and James 1979, Boness 1984, Anderson and Harwood 1985, Bishop et al. 2015c), novel behaviors are identified regularly but infrequently. Such behaviors are often peculiar to particular populations or colonies. On Sable Island, male gray seals were observed performing ‘yodel calls’ as part of their breeding aggression displays (Boness and James 1979). This vocalization was reported during the breeding season at other colonies in Nova Scotia (Schneider 1974) but appeared to be absent from male repertoires in the Eastern Atlantic (Boness and James 1979, Anderson and Harwood 1985). Similarly, in 2014 it was reported that male gray seals breeding at colonies along the eastern coast of England, UK (e.g., Donna Nook, Blakeney Point, and Horsey) were performing a ‘body slap’ behavior during aggressive contests that may be conveying information via acoustic signals or substrate vibrations (Bishop et al. 2014, Bishop et al. 2015a). Anecdotal observations suggest that this behavior was likely present since 1993 but had not been documented for over 20 years (Bishop et al. 2014).

In addition to breeding behaviors, isolated and novel foraging behaviors have been observed, with some suggestion of increased occurrence in recent years. In the Northeast Atlantic, there has been an increase since 2012 in reports of gray seals predating on marine mammals, including harbor porpoises, *Phocoena phocoena* (Haelters et al. 2012, Bouveroux et al. 2014, Jauniaux et al. 2014, van Bleijswijk et al. 2014, Haelters et al. 2015, Leopold et al. 2015a, b, Stringell et al. 2015), harbor seals, *Phoca vitulina* (van Neer et al. 2015), and even cannibalism of gray seal pups and juveniles (Bishop et al. 2016, Brownlow et al. 2016, van Neer et al. 2019). Observations of male gray seals exhibiting cannibalism have been reported in Canada (Bédard et al. 1993, Kovacs et al. 1996), but there were no further updates until the observations in Scotland (UK) and Germany (Bishop et al. 2016, van Neer et al. 2019).

It is tempting to suggest that the present reported surge in foraging on marine mammals reflects an increase in frequency or that the patterns reflect broader responses to ecosystem changes. Due to the opportunistic nature of the reporting of such behaviors, it is difficult to ascertain the role of sampling bias that might result from increased awareness and/or technological advances (e.g., DNA testing of wounds, Haelters et al. 2012). Nevertheless, these observations highlight a need for studies to explore the ethology of novel foraging strategies. As a data-rich species, gray seals provide considerable opportunity to explore the emergence, adaptive significance, and spread of behaviors through social or learned mechanisms. Capitalizing on the historical foundation of gray seal ethology and developing contemporary baselines for novel behaviors will be particularly important when there are direct conservation and management concerns. Recent examples are of gray seals raiding salmon traps (Königson et al. 2013), and mortalities associated with ‘corkscrew lesions’ that contribute to declines in localized harbor seal populations (Brownlow et al. 2016).

## 9.8 Future Directions

Ethological research on the gray seal has played a vital role in understanding a wide range of aspects of phocid ethology and behavioral ecology, as evidenced by the literature cited in the various chapters in section 1, such as reproductive behavior. In this chapter, we have endeavored to illustrate how research has grown from its early qualitative foundations through to quantitative analyzes addressing fundamental behavioral ecological principles that help to inform conservation and management practices, and that place gray seal behavioral research in a broader context.

Although gray seals can be regarded as a ‘data-rich’ species, compiling a review of the extensive literature allows one to identify limits of current knowledge and pinpoint areas of potentially productive future research (Fig. 9.12). For example, little is known about the mechanisms of learning in gray seals, the role of maternal effects on behavior beyond the direct provisioning of nutrients, or how physiological state might dictate an individual’s behavioral options. Perhaps the most challenging gap in our knowledge of gray seal ethology is how individual behavior patterns develop during early independence and prior to first breeding. Ultimately, we are seeking answers to the question of how much of gray seal behavior is controlled by nature and how much by nurture.

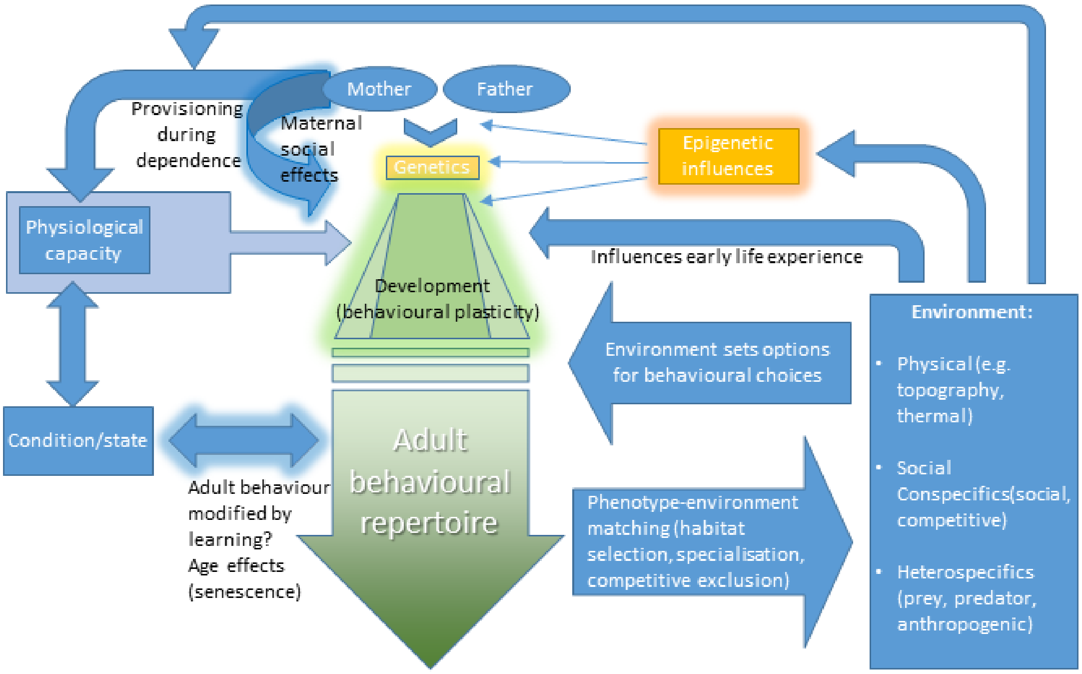


**Fig. 9.12.** Schematic summarising and synthesising the likely main drivers of an individual's behavioral repertoire. The elements with 'glowing' edges represent the areas/linkages that are currently unknown; the linkages between specific genotypes and behaviors, how behavior is shaped and modified during (post-weaning) development and the role of potential non-genetic maternal effects (e.g., social interaction). How development translates into the degree of behavioral plasticity is also unknown (represented by the width of the trapezoid; wider = more behavioral flexibility). Even once canalized, behavior is likely to be modified during adulthood, either through active learning processes, or constraint imposed by senescence. Although much is known about the environmental drivers of behavior (both on land and at sea), nothing is yet known about whether environment also plays a role through epigenetic effects.

The increased emphasis on intra- and inter-individual variation in behavior is providing a greater depth of understanding of gray seal biology, but we still have much to learn about what behavior is 'chosen', when and why, and from what suite of available options. Future research will require ever more synthetic and complex studies of known individuals over longer time periods that simultaneously test more parameters; such as the role of maternal social care or early-life stress, while also framing such analyzes in the context of opportunity for behavior, given physiological constraints and environmental possibilities. Studies will need to integrate more sophisticated and capable biotelemetry devices (e.g. McKnight et al. 2019) that monitor physiological change in real-time with more traditional behavioral observations (Fig. 9.13), and find ways to conduct ethical experimental studies that seek to manipulate behavior to test specific hypotheses.

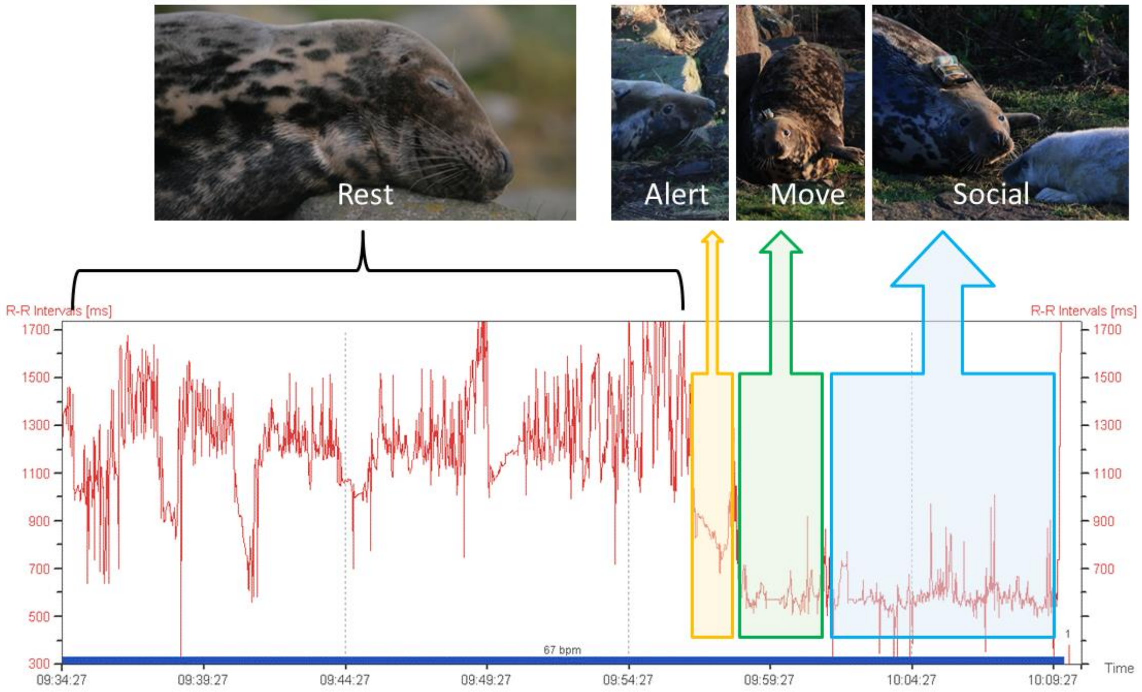


**Fig. 9.13.** An example of how integrating physiological and behavioral data at fine temporal resolution for individual seals can reveal more about the causes and consequences of behavior. Here, heart rate monitors deployed on lactating females on the Isle of May show how inter-beat interval (R-R interval in milliseconds) changes over a period of 35 minutes as a mother changes behavioral state. Initially, the mother is at rest near a pool approximately 15 m away from her pup, with long inter-beat intervals (equating to a low heart rate) with regular fluctuations. The female then becomes alert (yellow box), with a rapid reduction in inter-beat interval (heart rate increase), and then locomotes towards her pup (green box). Upon reunion with her pup, the mother engages in social interactions (mainly nosing; blue box) before proceeding to nurse the pup. Note the low inter-beat intervals (i.e., high heart rate) throughout the locomotion and social interaction phases (Twiss unpublished). Image credits: SD Twiss.

Behavioral adaptation is often an organism’s first line of defense against environmental perturbations and can be a key indicator of fundamental shifts in ecological processes. In a time of rapid environmental change and increased anthropogenic activities in both terrestrial and marine environments, it is vital to understand the ability of seals to adapt to these changes. Gray seal populations are undergoing range expansions and/or shifts in Eastern and Western Atlantic populations. This brings new challenges to the seals themselves, such as increased human interactions (e.g., gray seals in the Thames, UK, interactions with fish farms and fishing gear, interactions with sub-sea marine renewable energy devices) and changing ecosystem dynamics (e.g., white sharks and gray seals on the USA east coast, gray seals consuming porpoise and harbor seals). Understanding the processes of behavioral development and how individuals differ in their abilities to modify behavior patterns will be critical for effective planning of conservation and/or management strategies and predicting potential impacts of the gray seal as a top predator within a changing ecosystem.

The gray seal is a data-rich species but also presents an excellent study system for understanding phocid behavior and ecology, and broader ecosystem dynamics. As we have seen in this chapter, there has been a wealth of information gathered on gray seal behavior over the past 80 years, providing a solid understanding of many aspects of gray seal life-history, some in great detail such as their breeding behavior and ecology. The traits of this species that have enabled researchers to observe gray seals closely and examine the drivers of behavior are still relevant today: the variety of habitats they occupy, both on land and at sea, the ability to recognize and repeatedly observe and sample known individuals, and the ability to equip individuals with ever more sophisticated telemetry (e.g. McKnight et al. 2019) to provide windows into aspects of their life-cycle that are hidden from traditional behavioral observation. These traits will ensure that the gray seal remains a key study system, and the solid foundation of existing knowledge provides an ideal platform from which to investigate how individuals and populations cope with the pressing ecological and conservation issues of the twenty-first century.

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