PLAYING ON THE EDGE OF THE SEA: A COMPARATIVE ANALYSIS IN OTARIIDS AND ODOBENIDS

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Abstract

The role of play in the superfamily Otarioidea has not been widely explored. However, all the play types found in other so-called "playful groups" (e.g., primates or canids) have been reported among the sea lions, fur seals and walruses. Otariids and odobenids perform object play with animate and non-animate objects, such as kelp, rocks or seabirds. Locomotor-rotational play in otariids is mainly performed at sea, where animals exhibit complex and sophisticated movements such as pirouettes, torpedoes and somersaults. In the same family, play-fighting is the most common form of terrestrial social play, and it is composed of competitive behavioral patterns that are exchanged between players. As in other mammalian species, in otariids, play distribution follows a skewed bell-shape developmental curve, starting in infancy, peaking in juvenility and disappearing in adulthood. The distribution and modality of this behavior reflect the level of the sociality of a given species. In those species characterized by high levels of tolerance and maternal permissiveness, social play starts earlier in ontogeny. During play-fighting, play signals are displayed and exchanged between players in order to avoid escalating into aggression. In other mammalian taxa, the same signals have been reported and seem to serve the same purpose (e.g., Relaxed Open Mouth, "ROM"). In conclusion, testing hypotheses on the evolution of play requires that many species with diverse habits (e.g., terrestrial, aquatic, arboreal) and kinds of sociality (e.g., despotic, tolerant) are studied using a comparative perspective. Herewith, the superfamily Otarioidea can be an important piece to help understand this puzzling set of behaviors.

Keywords

Play-fighting, object play, locomotor-rotational play, play patterns, cooperative/competitive sessions, play signals, facial expressions, play in otariids, play in walrus, maternal styles.

Introduction

Play is a widespread behavior across many mammals (Burghardt 2005; Fagen 1981) and the species belonging to the superfamily Otarioidea are no exception. In these animals, play can be present from the very first phases of life and characterized by different types of play depending on the different species considered. For example, in otariids, pups begin to play with mothers, and then expand their playful spheres to other group members, especially peers (see Farentinos 1971). Play between newborns and mothers includes gentle bites that pups direct to the vibrissae, face and neck of the mother (Fig. 1). To reach the face of the mother, pups often climb over her back thus engaging in an energetically demanding activity (Fig. 2). From infancy to juvenility, social play becomes more complex and challenging. Play-fighting, the most vigorous form of play, is typical of youngsters, which confront each other by engaging in chest pushing, neck fencing and biting (Fig. 3). This type of playful activity requires an accurate control of movements and a sophisticated communicative system in order to avoid escalation into aggression. In many species of Otarioidea, social play is not the only type of play observed. Solitary play can also occur, and it can include both acrobatic motor actions and manipulative patterns (e.g., play with objects) (Fig. 4). Solitary play seems to be present in juvenile walruses (*Odobenus rosmarus*), which catch and repeatedly hit seabirds without eating them (Giljov et al 2017) (Fig. 5), and in Steller and New Zealand sea lions (*Eumetopias jubatus* and *Phocarctos hookeri*), which play with kelp by throwing it into the air and trying to grab it again (Marlow 1975).

All these authors described these activities as play. However, the main problem to tackle the topic of play relies on the difficulty of finding an appropriate definition of this behavior, which can be applied to all the species in which it has been studied.

Play behavioral patterns are recruited from different maintenance behaviors such as reproductive, aggressive or predatory activities. Moreover, the assemblage of the different behavioral patterns may vary according to the species' distinctive features, such as morphological traits, reproductive and social systems, and ecology. This high variability makes the operational definition of play difficult (Bekoff 2001; Palagi et al 2016; Pellis and Pellis 1996). Burghardt (2005) set up five criteria to define play that deal with the variability characterizing this peculiar behavior. To be categorized as play, a behavior has to fulfill the following criteria: i) it has to depart from being completely functional in the form or context in which it appears; ii) it should be rewarding and spontaneous; iii) it has to differ from its analogous functional behavior in form (exaggeration and rearrangement of motor actions) or in time (different ontogenetic stages); iv) it has to be performed repeatedly (absence of inhibition), but not stereotypically and v) it has to occur in absence of heavy environmental or social stressors (e.g., food shortage, social conflicts or presence of a predator threat).

Play between pups and their mothers in otariids, as described above, is a good example summarizing all these criteria. Climbing on and biting the mother i) is not functional (the behavioral pattern does not produce any kind of immediate benefit), ii) is spontaneous because the activity is initiated by the pup, iii) is limited to the first developmental stages, iv) is often repeated many times per bouts and v) occurs when energetic needs of pups are covered by mothers' milk.

Play can have both delayed (e.g., developing physical and cognitive skills, *motor training hypothesis*) and immediate benefits (e.g., creating and strengthening social bonds) (Byers and

Walker 1995; Smith 1997). However, play has immediate costs in terms of time, energy and survival (Fagen 1993; Harcourt 1991a; Palagi 2007).

The time spent in playful activities is subtracted from the time that could be spent in other essential activities (e.g., feeding, sleeping, mating). The percentage of time animals spend in playing differs across the different species in relation to their ontogenetic trajectories, personality, habits, diets and metabolic survival costs (Fagen 1993; Palagi 2018; DeRango and Schwarz, this volume). In some species, play represents a strong metabolic investment deriving from the physical effort (e.g., chasing playmates, acrobatic movements) (Fagen 1981). In juvenile Assamese macaques (*Macaca assamensis*), for example, the investment in locomotor play leads to reduced growth in both sexes (Berghänel et al 2015). This reduction is more accentuated in males that play more frequently than females and, consequently, grow less (Berghänel et al 2015). This suggests that play is an important factor in the developmental process, since it has ontogenetic priority over the physical growth rates.

Play also implies some risks. It increases the probability to be detected by predators especially when the intentional level of the subject is focalized on the playmate and not on the surrounding environment, as it occurs during play-fighting. Harcourt (1991a) quantified the number of attacks performed by South American sea lions (*Otaria flavescens*) towards immature South American fur seals (*Arctocephalus australis*). The author reported 102 attacks from which 26 resulted in kills, and 85% of these kills occurred when the immature pups were playing in the shadow tidal pools.

During their activity, players can be victim of injuries provoked by the playmates, and by the difficulty in the execution of some motor sequences (Harcourt 1991a). Mild injures can derive from falls and tumbles. During play-fighting, cheetah cubs often show signs of pain due to mild injures that can induce temporary impairment in the subject (Caro 1995).

Play can be expressed in a variety of modalities. Solitary play can occur either by manipulating objects/body parts or performing locomotor-rotational actions. During locomotor-rotational play, an animal repeatedly performs body movements in an exaggerated way such as running or torpedoing. These can be punctuated by rotational maneuvers such as body twisting, or somersaulting (Wilson and Kleiman 1974). Putting themselves in unnatural body/head positions in relation to gravity produces a strong limitation in sensory perception (Palagi 2014; Špinka et al 2001). This lack of physical and sensory control seems to be self-rewarding for the player, even though it involves a certain amount of risk (Pellis and Pellis 2009).

Object play differs from exploration at both, the functional and operational levels. When exploring, animals acquire information on their environment and familiarize with a novel object (Palagi 2014). In evolutionary terms, exploration is a *receptor* activity (*i.e.*, activity providing information about the unknown environment) which could have been favored by natural selection because of its survival functions (e.g., locating food, escaping from predators, exploiting the environment in an effective way). During object play, objects are used to create novel, uncertain, and challenging situations, which animals have to cope with (Špinka et al 2001). This is a self-rewarding activity that helps animals to assess and improve their motor and cognitive abilities (Palagi 2014). In this view, object play is an *effector* activity.

In sum, *receptor* activity of object manipulation contrasts with *effector* activity of object play in the sense that the former is focused on increasing familiarity with the object and creating the conditions to use it for adaptive purposes (e.g., I can take a melon never seen before, explore it, break it and eat it). The latter acts on the object, which can be already familiar, to use it in a way that can be totally disentangled from its intrinsic characteristics (e.g., I can take the same melon, roll it, jump on it while trying to maintain the equilibrium).

When two or more individuals interact in a playful manner, play becomes social. The most common form of social play in toddlers and non-human animals is play-fighting, which is characterized by offensive and defensive patterns that are generally balanced (Fagen 1981; Norscia and Palagi 2016). Obviously, animal play can involve a mix of activities. Locomotor–rotational play can involve the use of objects (e.g., kelp, sticks, branches) and it can be done in a social way. It is often difficult to disentangle each type of play from the other, since they can be performed together in sophisticated sequences forming a single natural category. Even though no single, simple definition of play category is satisfactory, such categorization helps ethologists identify, quantify and describe, in a standardized way, the different playful activities of animals (Burghardt 2005).

Play has been largely investigated in particular mammalian groups, especially primates, rodents, and canids. However, it has been less studied in other mammalian taxa such as marine mammals, probably due to the difficulty in following elusive animals in their natural habitats (Burghardt 2005, Hill et al 2017). This review deals with some aspects of solitary and social play of otariids and odobenids to take stock of the knowledge regarding play in these species. Moreover, we aim to explore play using a comparative perspective. To explore if there are some homologous traits in the shaping of play behavior, we will select species (e.g., harbor seals) that are phylogenetically close to otariids and odobenids but that differ from them in their mating systems and maternal styles. At the same time, to understand whether some traits of play can be shaped through a process of evolutionary convergence, we will look at those groups which are more phylogenetically distant from otariids and odobenids but that share similar mating systems and maternal styles (e.g., lowland gorillas, macaques). Due to the paucity of studies focusing on play in otariids and odobenids we will also discuss anecdotal reports.

One step before we ‘playfully’ jump into our target group

Demographic, natural and life history variables can influence play behavior (Ciani et al 2012; Cordoni 2009; Cordoni and Palagi 2016; Palagi 2007). Play in adults is often inhibited, while play in juveniles is very conspicuous (Fagen 1981). On the other hand, in species showing sexual dimorphism and/or sex differences in adult roles, play is often more frequent in males especially when adult competition for mates is high (Byers and Walker 1995; Fagen 1993). Play variability is affected by social features typical of the different species.

The mating system and social organization define the level of tolerance and proximity of individuals and, in turn, can shape play across group members (Palagi 2018). In polygynous species, male competition tends to be strong, and this may lead to vigorous fights to monopolize females (Cassini, this volume; Clutton-Brock and Huchard 2013; Emlen and Oring 1977). These aggressive adult tendencies may help explain the high levels of competition in juvenile play-fighting (Paquette 1994; Smith 1997). In this view, the most competitive players will likely have higher chances to gather high ranking status and, in turn, better reproductive opportunities in the future (Byers and Walker 1995). The so-called *motor training hypothesis* predicts that through play-fighting juveniles acquire and develop those physical and cognitive skills that will be useful in the future. In species, such as lowland gorillas (*Gorilla gorilla gorilla*), which are sexually dimorphic, male-male competition is common and adult play is usually inhibited due to the risk that play-fighting entails (Cordoni et al 2018). Nonetheless, adult play is frequent in tolerant species in which social relationships are not established and mediated through agonistic interactions and where the roles of males and females are well-balanced (e.g., bonobos, *Pan paniscus*, Palagi 2006; ring-tailed lemurs, *Lemur catta*, Palagi 2009).

Otariids and the walrus are sexually dimorphic species (Bones 1991) that share mating systems ranging from female-defense (males directly herd their females) to resource-defense polygyny (males defend the territory to attract females) (e.g., Bonin, this volume; Cassini, this volume;

Campagna and Le Boeuf 1988; Emlen and Oring 1977; Fay 1982; Le Boeuf 1991; Soto and Trites 2011). Except in Australian sea lions (McIntosh and Pitcher, this volume), females are highly synchronous and during the breeding season they congregate in specific areas. In otariid females, agonistic interactions are higher once they give birth, as the space for nursing their pups on land is reduced (Harcourt 1992a; Wartzok 2012). Males of both the Otariidae and Odobenidae families strongly compete to monopolize females, and individuals engage in fights that range from agonistic displays to violent confrontations with injuries. Conflicts occur within and between sexes, with males displaying coercive behaviors to retain and mount females. Aggression towards pups has also been described in otariids (Ryazanov, this volume; Campagna 2009). As the space for nursing is reduced, females display agonistic interactions towards alien pups in order to block their movements and may even kill them (Harcourt 1992b; Riedman 1990). In addition, infanticide by adult and juvenile males, although rare, has been reported in several species (e.g., Campagna et al 1988; Higgins and Tedman 1990; Ryazanov, this volume).

Taken together, all these features reveal the strong social competition of this superfamily involving (in some species) individuals of all age- and sex-classes. Such high levels of competition make this taxon particularly interesting to hypothesize about the role of mating systems and social organizations in shaping the distribution of play in terms of frequency and modalities. In particular, a comparative approach across the species could shed light on the potential benefits of play-fighting in developing those motor and social skills necessary to compete in adulthood.

Different maternal styles matter: the ontogenetic pathways of social play

Looking at the mother: mother-pup play

Maternal styles strongly affect the frequency and modality of infant social play in many mammalian species (Pellis and Pellis 2009). Therefore, it is mandatory to discuss play diversity in infants as a function of the role of the mothers in determining play attitude across the different developmental stages (Palagi 2018). Pinnipeds offer many possibilities to investigate the issue due to their extremely diversification in maternal styles. There are three main maternal strategies that have been described for pinnipeds: the ‘nursing aquatic strategy’, the ‘foraging cycle strategy’ and the ‘fasting strategy’ (Boness and Bowen 1996). In the ‘nursing aquatic strategy’, characteristic of the single odobenid species, the walrus, pups remain with their mothers wherever they go and are nursed both at sea and on ice (Fay 1982; Miller and Boness 1983). Lactation lasts 2-3 years, although pups start feeding autonomously at ~5 months of age (Boness and Bowen 1996). Otariids and a few species of phocids show the ‘foraging cycle strategy’. Females fast during the ‘perinatal period’ and later alternate between long foraging trips to the sea and short attendance periods at the colony to nurse their pups, with the consequence that pups can remain alone for long periods between maternal visits (Sepulveda et al, this volume). In these groups, lactation ranges from 4 months to 3 years. The remaining phocid species adopt the ‘fasting strategy’ with females who fast never separating from their pups for the whole lactation, which ranges from 5 to 50 days (though Weddell seals may be an exception to this rule, with some mothers diving to feed during lactation, leaving their pups on the ice (Wheatley et al 2008). It appears that the main difference across these three strategies is the amount of time that mothers spend with their pups until weaning, the energetic costs and the place used for nursing.

In the only species adopting the ‘nursing aquatic strategy’, the walrus, most social interactions between mothers and pups occur in the water and so they are particularly difficult to observe (Miller 1976), therefore, we cannot exclude that social play may be present in walruses. Otariid and phocid females are protective towards their offspring. They keep their pups in close proximity, preventing them from moving away or interacting with other individuals (Oftedal et al 1987). This precludes pups from interacting with peers and limits their interactions, including social play, just to their mothers (*social canalization*, Berman 1982). This phenomenon has also been described in macaque species with high levels of despotism and intraspecific competitiveness (Thierry 2004). Ciani et al

(2012) compared social play of immature subjects of two macaque species characterized by different levels of mother protectiveness and dominance hierarchy: the despotic Japanese macaque (*Macaca fuscata*) and the tolerant Tonkean macaque (*Macaca tonkeana).* The authors found that the former played at lower frequencies than the latter, thus suggesting a covariation between despotism and social play inhibition in immatures (*social canalization*).

In otariids, mother-pup play has been described in two species of sea lions (Steller sea lion, Farentinos 1971; Australian sea lion, *Neophoca cinerea,* Marlow 1975), and one species of fur seals (New Zealand fur seal, *Arctocephalus forsteri,* McNab and Crawley 1975) (see Table 1). This type of play is always initiated by pups and may differ over the course of lactation, becoming more complex and sophisticated when pups get older. During the first days of life, pups of New Zealand fur seals have been seen to mouth their mother's vibrissae and pass them over their head and nose (Fig.1). In the Steller and Australian sea lions, no play patterns have been reported in the first days of life, however, during the first weeks of lactation, pups have been observed to climb over the mother's neck biting at her face and head while she is in a reclined position (Fig. 2) (Farentinos 1971; Marlow 1975). In a play-fighting bout, the pup takes the aggressive role and the mother is almost always passive (e.i., self-handicapping strategy). The pup directs bites at its mother's cephalic region and neck, and the mother responds giving it back gentle bites. The bout ends when the mother pushes away her pup with her snout and moves her head away (McNab and Crawley 1975).

Looking at peers: pup-pup play

When otariid mothers make their feeding trips, they leave their offspring alone, leaving them free to interact with other pups. In some otariid species, pups gather in groups called "pods" in nearby areas where they spend most of their time resting and playing together (Farentinos 1971; Higgins and Gass 1993; McNab and Crawley 1975). The ontogenetic period in which inter-pup play starts differs across different species and depends on the time the mothers leave pups to make their first feeding trip after the perinatal period. New Zealand adult sea lions seem to be more tolerant towards alien pups than adults of other otariid species (Marlow 1975). For this reason, mothers may not be so protective towards their offspring. They remain with their pups and defend them during the first 2-3 days after birth, but soon after they leave them to move freely. Pups of this species are precocious and they move around and join other pups in large pods. Then they become more confident and play in small groups (polyadic play-fighting) at the edge of the sea at rock pools (Marlow 1975). In contrast to New Zealand sea lions, Australian sea lion pups are less precocious. Mothers leave their pups for the first feeding trip only 14 days after birth. At this time, pups remain alone and the only form of play they engage in is object play. At one month of age they become less diffident and join pods where they play-fight together in small groups (Marlow 1975). Considering the differences between the two species in the play developmental timing, it seems evident that maternal styles regarding mothers' protectiveness and foraging periods strongly influence pups' social interactions. This interpretation finds also support in Arnold and Trillmich's study on (1985) Galápagos fur seal (*Arctocephalus galapagoensis*). The authors highlighted the differences of pups' activities in presence and absence of their mothers and found a positive correlation between the amount of time spent in play-fighting and the amount of time they stayed separated from their mothers.

Play-fighting between pups is more complex than play-fighting in mother-pup dyads. For example, the number of players can increase and up to four pups may join a play bout (Arnold and Trillmich 1985; Farentinos 1971; Gentry 1974). In play-fighting, pups face off with their chests in contact and bite one another on their necks and cephalic regions (Farentinos 1971) (Fig. 6). Bites may also be directed at other body areas such as fore and hind flippers (Arnold and Trillmich 1985). While directing bites, playmates try to dodge the other's bites by moving their heads from side to side, as the apparent goal is to bite without being bitten (Gentry 1974). They sometimes grab the playmate's skin and vigorously shake their heads from side to side. Chest and neck pushing are also used as a tool to defeat the opponent. Short chases may also take place during play-fighting. All these patterns resemble the serious aggressive patterns that adult males engage in during the breeding season. In the Steller sea lion, play-fighting bouts can last more than 3-4 minutes, thus suggesting a strong energetic investment in such activity (Farentinos 1971).

Throughout the development pathway of pups, they become more agile and skillful, not only on land but also at sea. This implies that the time spent in engaging in activities under the water increases and makes more difficult the observation of pups and their monitoring. This is the reason why research on play behavior has only focused on early stages of pup development. The only study which shed light on the behavioral play types during the whole lactation period was carried out by Harcourt (1991b) in the South American fur seal. In this species, pups do not engage in social play until about 1 month after birth. Terrestrial social play in pups was only prevalent between the 1st and the 4th month of age, immediately after there was a strong increase in social swimming play that tended to gradually decrease until the end of the first year of life. Terrestrial and aquatic social play not only differ in their occurrence, but also in their form. In social play on land, animals engage in play-fighting, while at sea they mainly engage in locomotor-rotational play (e.g., chasing, pirouetting, somersaulting). The adaptability of social play to different environments across the ontogenetic stages clearly indicates the importance of this behavior in the achievement of skills which will be indispensable in the adult life (delayed benefits).

Towards maternal independence: play among juveniles

A substantial amount of social play can be found among juvenile otariids, however it has only been documented in four species of sea lions (Australian sea lion, Marlow 1975; New Zealand sea lion, Marlow 1975; South American sea lion, Llamazares-Martín et al 2017a; Steller sea lion, Farentinos 1971) and one species of fur seal (Cape fur seal, *Arctocephalus pusillus pusillus*, Caudron 1995) (see Table 1). Terrestrial play-fighting in juveniles does not strongly differ from that of pups even though the formers appear to be more coordinated and precise in their motor actions. Juvenile play lasts longer than pup play. For example, in Steller sea lions some play sessions are reported to last more than an hour (Farentinos 1971). However, juvenile play involves a higher level of roughness. Play in older juveniles and non-breeding males includes more aggressive elements and, sometimes, it escalates into overt aggression (Farentinos 1971; Marlow 1975) and this is probably the reason why in breeding males play is totally inhibited. In Australian sea lions, heavier juveniles repeatedly push their lighter playmates backwards until the play partners get away (Marlow 1975). Between matched partners, the more successful players are those whose competitive patterns are not dodged by the opponent (Fig. 3).

It has been demonstrated that the play-fighting style of a given species will be determined by its competitive nature and by the social benefits of play, being more imbalanced when it is useful for acquiring higher ranking positions, and well-balanced when it favors the creation and maintenance of social bonds (Pellis and Pellis 2016). In the South American sea lion, the only otariid species in which play-fighting style has been measured, play-fighting is well-balanced although it is rich in rough elements (Llamazares-Martín et al 2017a). Contrary to expectations, in this competitive species with low levels of social tolerance, play-fighting seems to have an important role in establishing and maintaining social relationships and it is predictive of the relationship quality of the subjects. Those animals that frequently engaged in play and, in particular, in well-balanced play sessions also shared strong affiliative relationships. The exchange of rough patterns during play-fighting may potentially lead to escalation towards aggression. In those species characterized by high aggressive tendencies and low levels of social tolerance play-fighting can become even riskier. Moreover, since rough play may lead to aggression, South American sea lions avoid engaging in play involving more than two players (polyadic play). However, when polyadic play takes place, the sessions have similar durations compared to dyadic sessions, suggesting that polyadic sessions are also well-managed. Moreover, in this species the level of balance characterizing the session seems to have an effect on play duration (Llamazares-Martín et al 2017a).

Male prevalence in play-fighting is especially important in juvenility, which is the last stage in which males have the opportunity to improve their fighting skills through play before reaching the breeding phase. In South American sea lions, juvenile male dyads play at higher rates than female dyads, and the latter play at lower rates than mixed dyads (Llamazares-Martín et al 2017a). Therefore, juvenile males of this species seem to motivate females to play. In the other three species of sea lions in which juvenile play has been reported, female play has never been observed (Farentinos 1971; Marlow 1975). A similar result has also been found in gorillas (Palagi et al 2007). Despite the large phylogenetic divergence between gorillas and the species of the superfamily Otarioidea, they share common social features that lead to similarities in the distribution and performance of social play. All these species show a marked sexual dimorphism and a polygynous mating system, in which males compete to monopolize and retain females (Watts 1991). As a whole, these findings suggest that similar social features concur in shaping similar play distribution in different species despite their phylogenetic distance.

Due to the risk of play-fighting in juveniles, sophisticated motor coordination and appropriate communication of the players' motivations are needed (Palagi et al 2016). This effective communication is mediated by messages that are conveyed through play signals. These signals consist of gestures and facial expressions that can be borrowed from other functional contexts and performed in a repetitive or exaggerated manner (Palagi et al 2016). By the performance of these signals, players point out the meaning of their subsequent actions specifying that "what follows is only play", thus clarifying players' motivation (Bekoff 2001; Pellis and Pellis 1996). A congruent reciprocity of play signals between the players is required to prolong the playful interaction. Signal reciprocity means that the receiver has appropriately codified the meaning of the signal and, by reproducing the same pattern, it expresses its agreement to prolong the playful interaction (Palagi et al 2014; Palagi and Mancini 2011).

The Relaxed Open Mouth (ROM) is one of the most widespread play signals across different taxonomic groups (primates, e.g., Palagi et al 2016, van Hooff and Preuschoft, 2003; rodents, Panksepp and Burgdorf 2003; carnivorans, e.g., Cordoni et al 2016, Poole 1978). It is a ritualized facial expression which derives from a biting action whose biting sequence has been inhibited (Fig. 7) (Palagi et al 2014; Tinbergen 1952). In otariids, it has only been anecdotally reported in the Cape fur seal (Caudron 1995) and studied in the South American sea lion (Llamazares-Martín et al 2017b). In the latter species, the Attempt to Bite pattern (PAB) was used as a control condition to test if ROM acts also as a play signal, since PAB shares very similar motor modules with the ROM. The communicative nature of ROM is indicated as there is a significant difference in the frequency in which ROMs and PABs were followed by real bites, thus suggesting that ROM is not a preparation to bite. That ROMs were more frequently reciprocated than PABs reinforces this hypothesis. In order to reach communicative effectiveness, a play signal has to be reciprocated (Fig. 8). In the South American sea lion, the interactive nature of the signal is confirmed when its reciprocity prolongs the duration of the interaction. In the South American sea lion, ROM was equally performed during dyadic and polyadic play, but was more reciprocated in dyadic sessions. The similar frequency of ROM in polyadic and dyadic interactions suggests that the motivation to play does not depend on the number of players involved. However, to reach an effective communication, play signals must be reciprocated by the receiver. The reciprocity of ROM reaches its peak in dyadic play, when there are more face-to-face interactions between the two players. This type of visual engagement favors the detection of the signal and, therefore, increases the probabilities that it may be reciprocated (Llamazares-Martín et al 2017b). Taken together, these results suggest that sea lions rely on visual signals for complex communication, since their reciprocity makes play more successful.

To be predator or a prey: the role of solitary play in developing future successful strategies

In our review on play, solitary play cannot be ignored because it is pervasive in many terrestrial and aquatic species (Burghardt 2005). As already mentioned, it can be categorized as play with objects or locomotor-rotational play.

In pinnipeds, when animals are confident at sea, they may perform swimming solitary play. Most sea lion species have been seen to perform bodysurfing (Eibl-Eibesfeldt 1984; R Harcourt, personal observation), that is when they ride a moving wave with their bellies, which carries them towards the shore. This behavior is repeated over again with no apparent goal, but adults usually perform it during storms to land high on the rocks (R Gentry, personal observation). Harcourt (1991b) reported that swimming solitary play patterns in South American fur seals resembled those that sea lions use when they escape from predators but did not provide a detailed description of the variety of patterns employed. Due to the paucity of the studies on solitary play in this superfamily, we cannot conclude that these are the only species, which perform swimming solitary play. On the other hand, in the superfamily Phocoidea, which is the closest phylogenetic group to Otarioidea, the only species in which swimming solitary play has been described is the harbor seal (*Phoca vitulina*, Renouf 1993; Renouf and Lawson 1986). In this species, swimming solitary play is composed of complex locomotor, rotational and acrobatic movements such as pirouettes, porpoises, or torpedoes. The striking similarity between locomotor-rotational patterns and anti-predatory movements in this and other mammal species suggests that the short- and long-term benefits obtained from engaging in these behaviors reside in the improvement of physical skills and motor coordination that would increase survival when animals must flee from predators (Špinka et al 2001). Moreover, since all pinniped species share similar morphological adaptations to the aquatic life and have similar anti-predator tactics, it is reasonable to think that several members of the Otarioidea superfamily perform solitary acrobatic play during their juvenile period.

Solitary object play can be performed with both inanimate objects and prey. Animals can also use their own body parts, especially the extremities, in a playful manner. The body parts become then "external" objects, which can provide stimuli for body exploration. In humans, for example, infants tickle their own feet and, sometimes, introduce their toes into their mouths and bite them (Rochat 1998). By playing with body parts at the beginning of their lives, animals, including humans, acquire the self-consciousness needed in the future for developing self-recognition. Moreover, this peculiar play practice favors motor coordination and performance of movements (Rochat and Hespos 1997). In Steller sea lions, pups may play with their fore or hind flippers. In the first case, they wave their fore flippers in front of their faces while attempting to catch them. Once pups have grabbed their flippers, they begin to repeatedly bite them. In the second case, pups approach their hind flippers to their heads while they are sitting upright and bite them following the same sequence (Farentinos 1971). These rudimentary actions of grabbing and biting body parts provide infants with somatosensory and proprioceptive information that may help them to recognize those body parts as theirs (Blanke 2012). The identification of the own body as a different object from those found in the environment (*ecological self*, Rochat 1998), derives from the double perception of stimuli acquired when two parts of the body are in contact. We could say that the player coincides with the playmate.

The most common and rudimentary version of solitary object play has been described in all the species of sea lions (Australian sea lions, Marlow 1975; Galápagos sea lions, Eibl-Eibefeldt 1955, California sea lions, Peterson and Bartholomew 1967; New Zealand sea lions, Marlow 1975; South American sea lions; C Llamazares-Martín, personal observation; Steller sea lions, Farentinos 1971) and in two species of fur seals (Cape fur seal, Caudron 1995; South American fur seal, Harcourt 1991b) (see Table 1). It is also common in captive juvenile Pacific walrus (R Harcourt, personal observation, Fig. 4). In this kind of play, animals manipulate (on land or at sea) inanimate objects such as rocks, feathers, sticks or pieces of kelp. When they play with a hard material object (e.g., rocks) they grab with their mouths and bite it several times (Eibl-Eibesfeldt 1955; Peterson and

Bartholomew 1967). When manipulating a soft or manageable material object (e.g., pieces of kelp), animals usually grab and hold it tightly, then they vigorously shake their heads from side to side. The objects may be tossed into the air and immediately grabbed again (Marlow 1975; Farentinos 1971). These behaviors bring to mind those performed when preying medium and big size animals, in which otariids firmly grab their prey by their teeth and quickly shake their heads from side to side (Hocking et al 2016, Hocking et al, this volume).

In certain cases, animals display preying maneuvers towards preys without feeding on them. This behavior has been defined as play since it loses its primary function, and because the patterns involved are strongly modified. The motor actions are slowed down, the predatory patterns are often interrupted and mixed with other behaviors and the sequences forming the session are frequently repeated without inhibition (Bonner and Hunter 1982; du Toit et al 2004; Giljov et al 2017). Such behavior has been reported in one species of sea lion (California sea lion, Riedman 1990), three species of fur seal (Antarctic fur seal, *Arctocephalus gazella*, Bonner and Hunter, 1982; and Cape fur seal, du Toit et al 2004, Marks et al 1997; Guadalupe fur seal, *Arctocephalus townsendi*, Riedman 1990) and the Pacific walrus (Giljov et al 2017). Antarctic fur seals were seen to kill penguins tossing them into the air, but rarely eating on them. Du Toit et al (2004) observed a similar behavior in Cape fur seals towards seabirds just after a feeding bout. Marks et al (1997), however, described some cases in which an adult fur seal seemed to teach several juveniles (1 and 2 years old) to prey on seabirds. Juveniles observed how the adult caught and degloved the animal and mimicked its behavior until they correctly performed it. The adult did not participate in those interactions, and in one of the cases, juveniles tossed the carcass into the air without killing the potential prey.

In the walrus, three main solitary playful interactions towards seabirds have been described (Giljov et al 2017). While approaching a seabird from the surface, a walrus can shake its head from side to side and splash its face and tusks against the water. During this behavioral sequence there is never physical contact between the two animals. In a second form of play, the walrus approaches the bird and when quite close, lunges towards it trying to hit it with its tusks. In a third form, the attack from below, the walrus approaches from below the surface trying to hit the bird with its tusks and to catch it in the mouth (Fig. 5). Despite the aggressive nature of the patterns described in the last two types of interaction, only one out of 51 birds was killed. This suggests that the behavior does not have any immediate benefits and is not functional for nutrition.

Walruses may also interact with seabird carcasses both solitarily or together with other individuals (social play). In the latter, an animal carries the carcass in its mouth. It brings the carcass close to another individual's head and subsequently pulls backwards the carcass. This behavior results in a play bout that usually continues after they lose their interest in the "object". This peculiar pattern strongly resembles that observed in many primate and canid species that is often defined as "capture the flag" (Palagi et al 2007). As in the case of the Cape fur seal, juveniles may acquire these preying techniques from adults or, as in the case of walruses, they may become skilled by directly interacting with the birds or their carcasses together with other juveniles or alone. Although seabird consumption may be opportunistic in otariids and odobenids, seabirds can be an important energy source during periods of food scarcity (Long and Gilbert 1997). In this perspective, playing with "potential prey" may be a scaffold to develop effective predatory strategies thus increasing survival opportunities in the future.

Conclusion

This review underlines that play behavior is present in the superfamily Otarioidea. Play relates to different patterns of behavior, depending on the species. Infant play is directly related to maternal attendance styles, which affects the development of social, cognitive and physical skills of the pup. An accurate monitoring of mother-pup early interactions (mother permissiveness, time spent with the pup and stimulating actions by the mothers) and the ontogeny of pup play in a more complex social environment would contribute to filling gaps related to this complex behavior.

Studying play in the wild is challenging. That is why the captive environment offers the opportunity to gather useful information in these kinds of studies. Management in captive settings is relevant because it allows evaluating the development of behavior under controlled conditions. For instance, in zoos and aquaria, lactation can be changed according to management requirements and, in some cases, the mother-pup dyad may be isolated from the group for several months thus, limiting pups' social interactions just to their mothers. Mother-pup isolation produces an artificial and complete social canalization, which is present when the mother exercises a control over the actions of the infant thus, limiting its social activity including play. The data collection carried out through the same observational methods on groups belonging to the same species living in structures with different kinds of management may provide opportunities to test hypotheses on the development of social and physical skills in the superfamily Otarioidea.

Another important point to test hypotheses on the evolution of play in a comparative manner is the number of species on which data should be collected. The selection should be done on the basis of their social features. Species differing in lactation, in the level of dimorphism, in the degree of social tolerance and in the ecological correlates should be followed and observed via similar methodological protocols to allow comparisons.

There is little knowledge of how pinnipeds communicate their motivations to play. Understanding how communicative systems modulate social interactions between subjects is fundamental to clarify some aspects of the social cognition of large-brained animals (Palagi et al 2016). For this reason, further data on the patterns that act as play signals are needed. In exploring these questions, we should be particularly attentive to the different sensory modalities through which the play message can be conveyed. We cannot exclude the possibility that, in otariids, more than one cue may be integrated in a multi-modal system to improve the significance of the message (Wierucka et al. 2018). It is possible that acoustic, olfactory and visual cues can be combined to optimize the transmission and decoding of the signal thus, making social playful sessions more successful. Due to the sophisticated abilities required to manage a playful session, many researchers consider play-fighting as a window into social cognition and a fertile field to explore cognitive skills.

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Figure captions

Fig. 1. Fur seal pup initiating a play session biting its mother's vibrissae. (Drawing by Daniele Santerini)

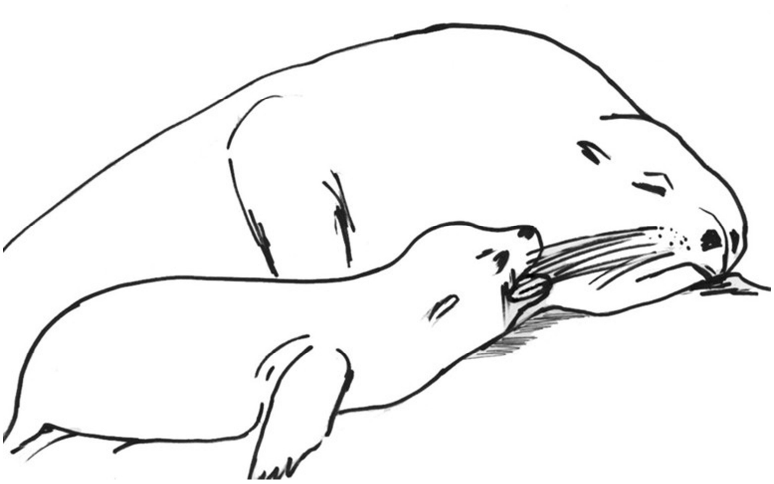

Fig. 2. Fur seal pup gently biting her mother's neck while climbing over its back. (Drawing by Daniele Santerini)

Fig. 3. Play-fighting in juvenile sea lions. The upper individual takes the dominant role by leaning on the belly of its playmate restricting its movements. The lower individual performs a Relaxed Open Mouth (ROM). (Drawing by Daniele Santerini)

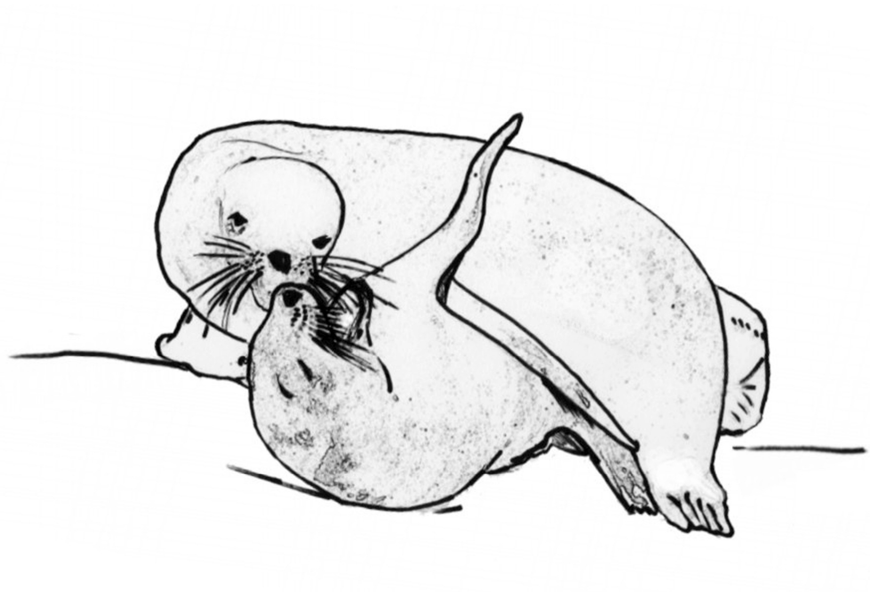

Fig. 4. Walrus performing object play with a ball. (Photo by Robert Harcourt)

Fig. 5. Failed attack from below performed by a juvenile walrus towards seabirds. (Drawing by Daniele Santerini)

Fig. 6. California sea lion pups biting their mouths. (Photo by Elisabetta Palagi)

Fig. 7. California sea lion pups reciprocally displaying a Relaxed Open Mouth (ROM). (Photo by Elisabetta Palagi)

Fig. 8. California sea lion pups displaying a reversed Relaxed Open Mouth (ROM). (Photo by Tommaso Ragaini)