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Prospective evolutionary drivers of allocare in wild belugas

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Abstract

Allocare, investment in offspring from non-parents, poses an evolutionary enigma. While the fitness trade-offs driving parental care are universal, alloparents may be driven by kin selection, reciprocation, the need to acquire parenting skills ('learning-to-parent'), an indiscriminate attraction towards infants ('natal attraction'), or a combination of multiple drivers. Among belugas (*Delphinapterus leucas*), allocare has been reported in wild and captive populations, but its underlying mechanisms remain untested. Using over 1800 focal observations, we quantified alloparental associations in St. Lawrence Estuary (SLE) belugas to determine whether the learning-to-parent and natal attraction hypotheses are consistent with patterns of allocare in this population. We found that subadults showed little interest in providing allocare and that alloparental investment remained constant across offspring age classes. As the observed patterns of allocare are inconsistent with both the learning-to-parent and natal attraction hypotheses, allocare in SLE belugas is likely driven by kin selection, reciprocation, or a combination thereof.

Keywords

allocare, alloparental care, beluga, kin selection, learning-to-parent, natal attraction, reciprocation.

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1. Introduction

Parental care is a limited resource, and allocations of care therefore reflect an evolutionary trade-off (Trivers, 1972). However, in some species offspring receive allocare, care from other group members, known as alloparents, in addition to parental care (Riedman, 1982). Alloparents provide care through allonursing, food-provisioning, infant-carrying, allogrooming, and protection from predators and hostile conspecifics (Blaffer Hrdy, 1976). For example, female wedge-capped capuchins (*Cebus oliveceus*) nurse each other's young (O'Brien & Robinson, 1991), African elephants (*Loxodonta africana*) assist, comfort, and protect all calves within their family unit (Lee, 1987), and sperm whales (*Physeter macrocephalus*) take turns escorting calves during maternal foraging dives (Whitehead, 1996). Like parental care, allocare is understood to reflect an evolutionary trade-off. However, while parents provide care to promote their own direct fitness, this is not always the case for alloparents.

Several hypotheses seek to explain the adaptive value of allocare for alloparents. When alloparents are related to recipient offspring, alloparents should provide care if the inclusive fitness benefits of allocare are greater than the cost to their future reproduction (the kin selection hypothesis; Hamilton, 1964; Trivers, 1972). Alternately, alloparents may provide care to offspring with the expectation of receiving some benefit in return (the reciprocation hypothesis; Trivers, 1971, 2006). The exact conditions necessary for reciprocation behaviour have been extensively debated (Rothstein & Pierotti, 1988; Symons, 1989; Carter, 2014), but here we consider that any benefit that alloparents receive as a result of allocare are reciprocal benefits. Allocare may also be adaptive when group members have improved fitness in larger groups, such that alloparents benefit by helping the offspring of others reach maturity, a form of delayed reciprocation (the group augmentation hypothesis; Kokko et al., 2001). In some species, young alloparents may provide care to offspring to gain parenting experience, thereby gaining future fitness benefits (the learning-to-parent hypothesis; Fairbanks, 1990). Finally, allocare may result from an indiscriminate attraction towards infantile traits (the natal attraction hypothesis; Silk, 1999). In this case, natal attraction favours parental behaviour, but sometimes results in misallocations of care. For both the learning-to-parent and natal attraction hypotheses, any benefit to offspring is incidental, a form of by-product beneficence (Rothstein & Pierotti, 1988).

Importantly, none of the hypotheses described above are mutually exclusive. For example, caring for kin in one's social group may provide both group augmentation benefits and inclusive fitness benefits (Kokko et al., 2001). In addition, natal attraction and learning-to-parent may be closely linked if an attraction to newborns compels subadults to provide allocare, thereby improving their parenting abilities (Silk, 1999). While some have specified that, by its definition, allocare must benefit offspring (Woodroffe & Vincent, 1994), others consider that allocare need not occur for the offspring's benefit and may in fact be detrimental to offspring in some instances (Blaffer Hrdy, 1976; Fairbanks, 1993). Given that neither the learning-to-parent nor the natal attraction hypotheses imply benefits for offspring, we consider that allocare can be defined as any interaction or association between an offspring and a non-parent that carries some cost to the non-parent (Mann & Smuts, 1998).

The evolutionary mechanisms underlying allocare among primates have been closely examined in past decades (e.g.: Lancaster, 1971; Blaffer Hrdy, 1976, 2011; Quiatt, 1979; Fairbanks, 1990), and there is increasing interest in characterising allocare among the social odontocetes, i.e., toothed whales. Allocare has been reported among bottlenose dolphins, (*Tursiops* spp.; Mann & Smuts, 1998), Atlantic white-sided dolphins (*Lagenorhynchus acutus*; Simard & Gowans, 2004), harbour porpoises (*Phocaena phocaena*; Anderson, 1969), orcas (*Orcinus orca*; Haenal, 1986; Waite, 1988), sperm whales (Whitehead, 1996; Gero et al., 2013; Konrad et al. 2018), long-finned pilot whales (*Globicephala melas*; Augusto et al. 2017) and belugas (*Delphinapterus leucas*; Bel'kovitch & Sh'ekotov, 1993; Leung et al., 2010; Hill & Campbell, 2014; Krasnova et al., 2014). As long-lived animals living in a difficult-to-access environment, it is particularly challenging to investigate the evolutionary drivers of allocare in odontocetes. However, evidence suggests that odontocete alloparents are driven by a mosaic of possible benefits. Among sperm whales, kin selection and reciprocation are likely drivers of allocare, although learning-to-parent and group augmentation may also play a role (Gero et al., 2013; Konrad et al., 2018). Among orcas, male alloparents selectively care for related offspring, while female alloparents (primarily subadults) care for both related and unrelated offspring, possibly to gain parenting experience (Waite, 1988). Among bottlenose dolphins, allocare is likely driven by natal attraction and learning-to-parent, although kin selection has not been ruled out as a possible driver (Mann & Smuts, 1998). Augusto et al. (2016) suggest that allocare among long-finned pilot whales carries little to no cost for alloparents and may therefore arise as a by-product of their social structure, but did not consider the energetic costs of escorting offspring.

Among odontocetes, formation locomotion describes dyadic formations between adult 'escorts' and offspring that are hydrodynamically costly to escorts, but advantageous to offspring (Weihs, 2004; Hill & Campbell, 2014). Analogous to infant-carrying in terrestrial animals, formation locomotion carries energetic costs for escorts (Noren, 2008). Two types of formation locomotion are typically described among odontocetes: echelon position, where offspring are maintained near the escort's mid-lateral flank (Noren et al., 2008, Figure 1A) and infant position, where offspring swim directly beneath the escort's tail (Noren & Edwards, 2011, Figure 1B). Although echelon position greatly facilitates offspring locomotion, it is highly costly to escorts. A bottlenose dolphin calf in echelon position receives 60% of its thrust from its escort, which sees its maximum swim speed reduced by 24% due to additional drag (Weihs, 2004; Noren, 2008). In contrast, infant position confers smaller hydrodynamic benefits to offspring and is energetically less costly to escorts, but may function to camouflage offspring from predators, provide comfort in high-stress situations, and facilitate nursing (Noren & Edwards, 2011).

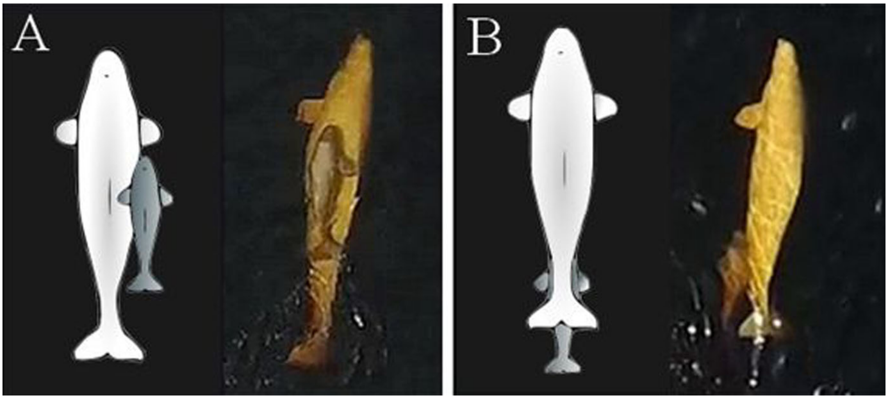

Figure 1. Formation locomotion positions typical of offspring care among belugas and other odontocetes, depicted as dorsal-facing diagrams and as seen from uncrewed aerial vehicle (UAV) footage. (A) Adult with calf in echelon position, an energetically costly care behaviour. (B) Adult with calf in infant position, a relatively less costly care behaviour offering social and anti-predator benefits.

Among belugas (*Delphinapterus leucas*), allocare has been described in captive animals (Leung et al., 2010; Hill & Campbell, 2014), and anecdotally reported in wild populations (Béland et al., 1990; Bel'kovitch & Sh'ekotov, 1993; Krasnova et al., 2014), but the evolutionary drivers of allocare in belugas remain untested. Preliminary reports of allocare in White Sea belugas suggest that, like bottlenose dolphins, beluga allocare may be driven by learning-to-parent and natal attraction. Bel'kovich & Sh'ekotov (1993) report observing 'kindergarten groups', where immature individuals cared for calves while their mothers were foraging. Similar to bottlenose dolphins, evidence suggests that belugas live in sexually segregated fission-fusion societies characterized by labile group membership (Loseto et al., 2006; Michaud, 2006; Alekseeva et al., 2013; Krasnova et al., 2014). Offspring remain dependent on their mothers for several years (Matthews and Ferguson, 2015). Male offspring eventually disperse from groups of females and form close bonds with other males that may last several years (Michaud, 2005), although the average age of male dispersal remains unknown. Evidence suggests that adult females associate preferentially with kin (Colbeck et al. 2013), but most female groups contain both related and unrelated individuals and are not matrilineal in nature (O'Corry-Crowe et al., 2020).

1.1. Hypotheses and predictions for the evolution of allocare in SLE belugas

Through a sustained effort targeting belugas with offspring in the St. Lawrence Estuary (SLE) beluga population, we quantified alloparental associations to determine whether allocare among SLE belugas is consistent with two non-mutually exclusive hypotheses: the learning-to-parent hypothesis and the natal attraction hypothesis.

1.1.1. The learning-to-parent hypothesis

When allocare results in future fitness benefits for alloparents through learning-to-parent, we expect that most alloparents should be immature females nearing breeding age (i.e., subadults), given that caring for infants typically only improves the fitness of reproductively inexperienced mothers (Fairbanks, 1990). Simultaneously, these subadult allomothers should favour infants, as we expect that contact with infants, more so than older offspring, will improve an allomother's parenting abilities and future reproductive success, given that this is when offspring are most vulnerable (Mann

Table 1.
Proposed hypotheses for the evolution of allocare among St. Lawrence Estuary belugas.

Hypothesis	Subadult allomothers over-represented?	Relationship between offspring age and alloparental investment		
		Association duration	Echelon swim duration	Infant swim duration
Learning-to-parent	Yes	–	–	+
Natal attraction	No	–	–	+

The learning-to-parent hypothesis predicts that female subadults will be over-represented compared to other alloparents, and that alloparental investment will decline with offspring age, as evidenced by a decrease in association duration and echelon swim duration coupled with an increase in infant swim duration. The natal attraction hypothesis predicts that both adults and subadults will provide allocare, and that alloparental investment will decline as offspring age. Alloparental investment was estimated as a function of association duration, echelon swim duration, and infant swim duration.

& Smuts, 1998). Therefore, we expect that the duration of alloparental associations (the total time spent by an alloparent in formation locomotion or in physical contact with recipient offspring) will decrease as recipient offspring age increases. Concurrently, we also expect that the duration of alloparental infant swims (a low cost behaviour) will increase and the duration of alloparental echelon swims (a high cost behaviour) will decrease as offspring age increases (Table 1).

1.1.2. The natal attraction hypothesis

The natal attraction hypothesis places no constraint on alloparent age, as individuals of any age or reproductive state can experience natal attraction (Mann & Smuts, 1998). However, natal attraction allocare should decrease as offspring age, due to the progressive loss of infantile traits as offspring mature (Bădescu et al., 2015). Therefore, if natal attraction drives allocare in this population, then both subadults and adults should provide allocare, and we expect to see shorter alloparental associations and shorter echelons swims, coupled with longer infant swims, for older recipient offspring.

2. Methods

2.1. Obtaining footage of belugas with offspring

We conducted fieldwork in the summers of 2016 to 2018 (Table 2). Using uncrewed aerial vehicles (UAV; Phantom 4 and Phantom 4 Pro, DJI, Shen-

Table 2.

Summary of sampling effort of maternal and alloparental associations among belugas in the St. Lawrence Estuary, showing the sampling period for each year, the number of sampling days, the total number of UAV flights per year, mean video duration by year, and the total duration of all videos obtained per year, including footage where no focal follows were recorded.

Year	Start date	End date	No. of Sampling days	No. of UAV videos	Mean video duration ± SD (min.)	Total video duration (h)
2016	07/16	09/22	18	61	13.4 ± 5.5	13.7
2017	06/25	08/12	16	58	15.6 ± 4.4	14.4
2018	07/08	08/19	22	60	17.8 ± 3.2	16.9
Total	–	–	56	179	15.6 ± 4.8	45.0

zhen, P.R. China) we obtained footage of SLE belugas with offspring. Sampling occurred in the Saguenay River, between the mouth of the Saguenay and Baie Ste-Marguerite, in Quebec, Canada (Figure 2). Baie Ste-Marguerite is a portion of the SLE beluga summer range that is heavily used by groups of females with young in the summer (Pippard & Malcolm, 1978; Michaud, 1993). Due to the sexually segregated nature of beluga sociality (Michaud, 2006), most of the recorded adults were likely female, but we made no attempt to sex observed individuals. Whenever possible, we followed groups that included multiple offspring, and systematically followed groups with younger offspring when larger groups split, always attempting to follow the same group as long as possible. We launched the UAV from the deck of an 8 m rigid-hulled inflatable vessel from 16 July 2016 to 22 September 2016, and from 3 July 2017 to 11 July 2017. On 26 June 2017, we constructed a scaffolding tower in Baie Ste-Marguerite to be used as a fixed UAV launch point. We erected the tower over the course of a few hours during a neap tide, when belugas were absent from the area. We launched the UAV from this structure from 20 July 2017 to 12 August 2017 and from 8 July 2018 to 19 August 2018. By using the research tower, we aimed to minimize the impact of the study on the behaviour of the study subjects. Noise from watercraft is an important source of disturbance to odontocetes in general (Erbe, 2002; Williams et al., 2006), and SLE belugas specifically (Lesage et al., 1999; Scheifele et al., 2005).

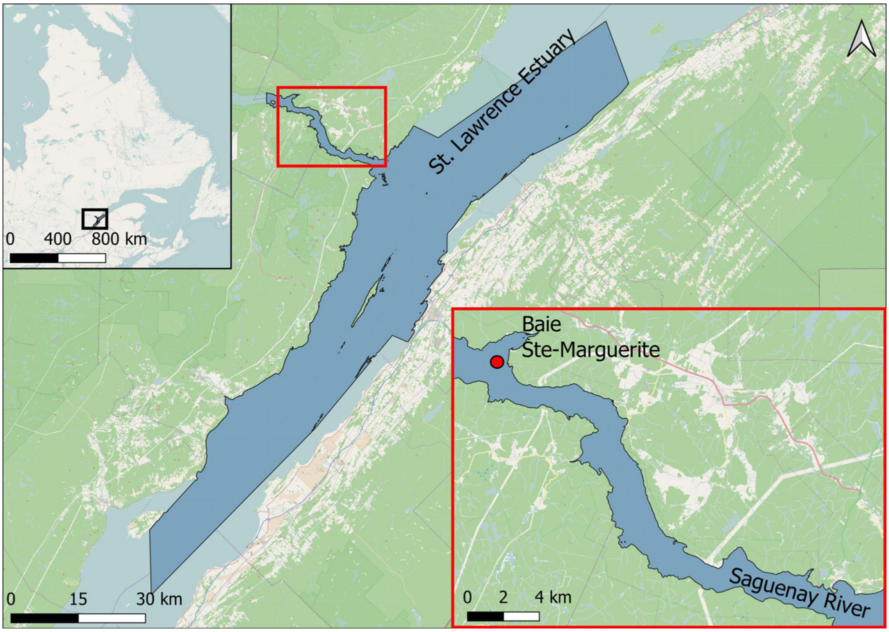

Figure 2. Critical habitat of St. Lawrence Estuary belugas in Quebec, Canada, according to the Department of Fisheries and Oceans (DFO, 2012). The lower right-hand inset shows the extent of the study site, from the mouth of the Saguenay River to Baie Ste-Marguerite. The red circle shows the approximate location of the research tower. In 2016 and 2017, sampling occurred in the Saguenay River and Baie Ste-Marguerite. Sampling in 2018 occurred in the Baie Ste-Marguerite area exclusively.

2.2. *Ethical note*

Our fieldwork methods were reviewed and approved by the Memorial University Animal Care Committee (Animal Use Protocol: 20190640). Our research, and specifically, the use of research UAVs in the Saguenay St. Lawrence Marine Park was covered by research permit SAGMP-2018-28703 issued by Parks Canada and QUE-LEP-001-2018 issued by Fisheries and Oceans Canada. At all times, we maintained the UAV at an altitude greater than 20 meters to avoid disturbing the study subjects, as low altitude UAV flights are more likely to disturb marine mammals (Smith et al., 2016). We noticed few apparent reactions to the UAV. More recent studies suggest that a minimum altitude of 30 m is advisable for studies of marine mammals (Ramos et al., 2018; Fetterman et al., 2019; Raoult et al., 2020), but our data collection predates these recommendations.

2.3. Continuous behavioural focal sampling of beluga offspring

Following Altmann's (1974) recommendations for continuous behavioural focal sampling, we systematically conducted focal follows for all offspring recorded in UAV footage. Offspring were sorted into three age classes: calves (approx. 0–4 months, Figure 3A), yearlings (approx. 12–16 months, Figure 3B), and juveniles (approx. 2–5 years, Figure 3C). While colouration is often used to estimate the age of beluga offspring (Krasnova et al., 2012, 2014), the appearance of colour varied considerably with light conditions and camera settings. Therefore, we mostly relied on visual estimates of the size of offspring relative to adults and their behaviour to assign age classes. Calves were approximately one-third the length of an adult beluga, with dark pigmentation around the blowhole, fetal folds often still apparent and noticeably 'clumsy' swimming behaviour. Yearlings were larger than calves but less than half the size of adults, with a very plump profile and more agile swimming behaviour than calves. Juveniles were between half and three quarters of the length of an adult beluga, with a more streamlined profile than yearlings. We also differentiated subadults (approx. 6–12 years) from adults (Figure 3D). We considered that subadults were likely fully independent from their mothers, but not yet sexually mature (Robeck et al. 2005). Subadults were between three-quarters to almost full adult length but

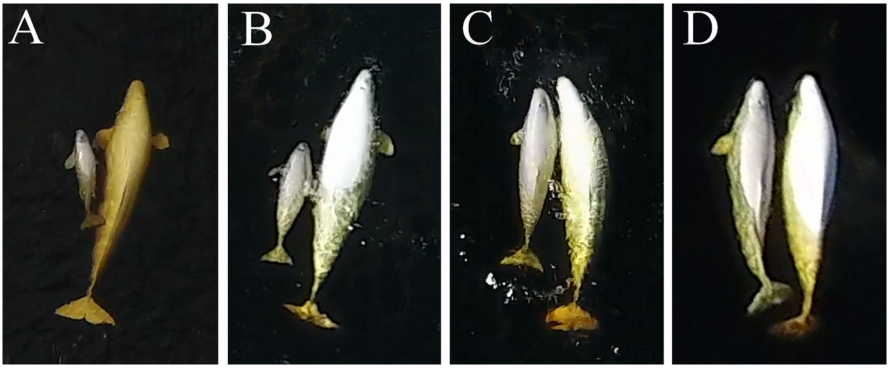

Figure 3. Comparing four age classes of immature St. Lawrence Estuary belugas relative to adults. (A) Calf, approximately one third adult length with dark pigmentation surrounding blowhole. (B) Yearling, approximately half adult length, plump, barrel-like profile. (C) Juvenile, half to three-quarters of adult body length with more stream-lined profile than yearlings. (D) Subadult, three-quarters to almost full adult length but noticeably slimmer and darker than adult.

were noticeably slimmer than adults. In almost all light conditions subadults appeared light grey, while adults always appeared white.

A focal follow consisted of the entire duration of time that a focal offspring remained in sight or could be distinguished from other offspring. When multiple offspring were present in a single group, we reviewed the footage multiple times until the behaviour of all focal offspring had been analysed. As many offspring were visible for only a few seconds, we discarded focal follows lasting less than 10 seconds to avoid inflating the dataset with uninformative focal follows. Seen from our UAV footage, belugas lacked individually distinguishing features, so each new offspring observation was recorded as a new focal follow. To account for resampling of the same individuals, we included the video number as a random effect in our models. To verify that we were not resampling the same group of belugas each day, we checked the frequency of re-observation of photo-identified individuals in the study site during the study period (see Appendix A). We conducted behavioural analysis of focal follows with the event recorder JWatcher 1.0 (Blumstein & Daniel, 2007).

2.4. *Quantifying escort associations*

We considered that maternal or alloparental associations occurred when adult or subadult ‘escorts’ swam in echelon or infant position with offspring, or otherwise maintained physical contact with offspring. According to Weihs (2004), bottlenose dolphin calves benefit from echelon position when the distance between mother and calf is less than the sum of half of the mother’s thickest cross-section and half the calf’s thickest cross-section. We considered that offspring were in echelon position if they were roughly within this distance of an escort (estimated visually), with synchrony in directional change. We considered that offspring were in infant position if they were positioned directly beneath the escort’s tailstock and showed synchrony in directional change. We counted the number of escorts associated with each offspring, maintaining a conservative estimate by counting a new escort only when we could visually confirm that it was not a previously counted escort. We calculated the total duration of each association by summing the duration of time that an escort swam with a focal offspring in echelon or infant position or maintained physical contact with the offspring. We also calculated the total duration of each association spent in echelon or infant position. For a subset of 32 videos obtained in 2018, we assessed whether each association was initiated by the focal offspring or its escort. Following our statistical analysis, we also re-examined each association involving a subadult escort to determine whether each of these associations was initiated by the focal offspring or the subadult escort.

2.5. Assigning mothers and alloparents

Since we did not collect genetic data to assign maternity genetically, we relied on behavioural observations to assign assumed maternity. When offspring only associated with a single adult escort, we assigned maternity to this escort. When offspring associated with multiple adult escorts, we assigned maternity to the escort that spent the greatest proportion of the focal follow with the focal offspring, based on the observation that beluga calves in captivity spend most of their time swimming with their mothers (Hill et al., 2013; Hill & Campbell, 2014). We designated all other adult escorts as alloparents. We also categorized all subadult escorts as alloparents, as these individuals were likely sexually immature and therefore unlikely to be mothers.

We tested the reliability of these methods using observations of a readily identifiable mother (with a deep scar on her left flank) and juvenile (with a distinctive spinal deformity). The mother has been followed through photo-identification since 1987, and the juvenile was first observed accompanying the mother as a newborn in 2014 (Robert Michaud, unpublished data). The pair have been resighted together every year since, leaving little doubt about their mother-offspring relationship. In 2017, we observed this juvenile six times over two sampling days. In all focal follows, our methods correctly identified the juvenile's mother.

2.6. Interobserver reliability analysis

To ensure the reliability of the main observer (JAA), we trained two secondary observers to re-analyse a subset of the videos. These observers respectively analysed 11 and 17 videos, for a total of 28. For all variables of interest, we compared their observations to JAA's observations using the intraclass correlation coefficient (Koo & Li, 2016). See Appendix B for more details.

2.7. Comparing adult and subadult alloparents

To obtain a representative estimate of the number of potential subadult allomothers available to offspring, we counted how many adults and subadults were observed in all groups, in each video taken during the 2017 sampling season. All videos began with a brief, high-altitude survey of the groups in the area, which was ideal for taking counts. We did not attempt to correct for underwater animals, counting only animals visible at the surface. Conservatively assuming that half of the observed subadults were female, ignoring any possible subadult male dispersal, we calculated the percentage of available alloparents that were subadult females. We used a chi-squared goodness of fit test to determine whether the observed proportion of subadult alloparents was greater than expected given the abundance of female subadults in the study area.

2.8. Comparing maternal and alloparental investment across age classes

We constructed three generalized linear mixed-effect models to compare the impact of offspring age on the duration of escort associations, echelon swims, and infant swims, for both maternal and alloparental associations (Table 3). Maternal associations were included in the models to verify that the metrics used to describe investment showed the expected pattern of declining maternal investment as offspring aged (Trivers, 1972). Each model was provided with a dataset where each row represented a maternal or alloparental association. Each row included an 'escort association duration' (always greater than zero), an 'echelon swim duration', an 'infant swim duration' and whether the escort was a mother or an alloparent. Focal follow ID was included in all models as a random effect, as offspring that received

Table 3.
Generalized linear mixed models used to test how maternal and alloparental investment in SLE belugas varied with offspring age class. Association duration was defined as the total time that an escort was in physical contact with an offspring or engaged in echelon or infant swimming with an offspring. All three models were identical except for the response variable.

	Model		
	Association	Echelon	Infant
Response variable	Association duration (s)	Echelon swim duration (s)	Infant swim duration (s)
Fixed effects	Offspring age (calf, yearling, or juvenile), Escort type (mother or alloparent)		
Interaction	Offspring age × Escort type		
Random effects	Year, Video, Focal follow		
Offset	Scaled focal follow duration		

allocare were represented in multiple rows. ‘Video’ was also included as a random effect to account for possible resampling of the same focal offspring within the same video. We included sampling year as a random effect to account for variation in sampling methods across years. Focal follow duration was included as an offset because offspring with longer focal follows were likely to have longer associations. We checked the residuals for all three models for normality and found them acceptable. We conducted Tukey post-hoc tests to check for significant differences between age classes, for both mothers and alloparents, for all three models. We then used the obtained intercept and coefficients for each model to estimate the duration of each behaviour for each combination of offspring age and escort type. We carried out all analyses in the R environment (version 3.4.3; R. Core Team, 2013) with the lme4 package (Bates et al., 2015) and the emmeans package (Lenth et al., 2020).

3. Results

3.1. *Inter-observer reliability analysis*

The interobserver analysis suggested that JAA’s observations were reliable. For the 28 videos analysed, all variables compared showed moderate to excellent agreement between JAA and the two secondary observers. Koo & Li (2016) consider that intraclass correlation coefficient values lower than 0.5 reflect poor reliability, values between 0.5 and 0.75 represent moderate reliability, values between 0.75 and 0.9 reflect good reliability, and values greater than 0.9 reflect excellent reliability. The lower bound of all our intraclass correlation coefficients 95% confidence intervals were greater than 0.5 and are therefore acceptable under these guidelines (Table 4). For more details, see Appendix B.

3.2. *Summary of focal follows*

In total, from 179 UAV videos, we recorded and analysed 465 calf focal follows, 211 yearling focal follows, and 1190 juvenile focal follows, for a total of 1866 focal follows (Table 5). Most, but not all focal follows included a maternal association. The long average duration of calf focal follows, and proportionally high number of allomaternal associations observed is likely due to the poor diving ability of calves, which results in greater observability at the surface. All measurements of mean duration include very large

Table 4.
Correlation coefficients with confidence intervals comparing JAA's observations to two secondary observers across a subset of 28 videos.

Variable of interest	Intraclass correlation coefficient [95% CI]
Association duration	0.91 [0.79, 0.96]
Echelon swim duration	0.84 [0.64, 0.93]
Infant swim duration	0.81 [0.57, 0.91]
Number of calves	0.93 [0.84, 0.97]
Number of yearlings	0.89 [0.77, 0.95]
Number of juveniles	0.81 [0.60, 0.91]
Number of escorts	0.87 [0.71, 0.94]

standard deviations, demonstrating high variability in the observability and duration of associations even within age classes. Of 1866 focal follows, 257 (13.7%) showed evidence of allocare, with offspring either associating with subadult escorts, or with multiple adult escorts. In the 32 videos where we systematically determined whether associations were initiated by focal offspring or escorts, we found that the majority of associations for which the initiating individual could be identified were initiated by offspring. Approximately 86.2% of maternal associations ($N = 58$), and 83.3% of allomaternal associations ($N = 12$) were initiated by offspring. Overall, most offspring,

Table 5.
Summary of all focal follows analysed across three offspring age classes for SLE belugas, for both maternal and alloparental associations. An association was considered to occur when offspring were in physical contact with an escort or engaged in echelon swimming or infant swimming with an escort.

	Number of focal follows	Mean focal follow duration ± SD (s)	Maternal		Alloparental	
			Number of associations	Mean association duration ± SD (s)	Number of associations	Mean association duration ± SD (s)
Calf	465	132.8 ± 162.6	431	97.2 ± 121.6	107	26.9 ± 38.3
Yearling	211	86.7 ± 105.8	195	60.2 ± 66.9	20	22.6 ± 25.0
Juvenile	1190	69.7 ± 81.5	1058	48.9 ± 57.5	130	17.9 ± 23.3
All age classes	1866	87.4 ± 113.2	1684	62.5 ± 82.4	257	22.0 ± 30.8

including very young calves, initiated associations with their mothers and alloparents.

3.3. Role of subadult alloparents

In focal follows where allocare occurred, 309 alloparents were observed, of which 300 were adults, and 9 were subadults. In 2017, we recorded 107 observations of subadults and 1230 observations of adults. We therefore consider that subadults represented approximately 8% of available alloparents. Conservatively assuming that half of the subadults observed were female, female subadults, therefore, represented 4% of available alloparents. Results from the chi-squared goodness of fit test showed that the observed number of subadult alloparents was not significantly different than expected based on the abundance of subadult females ($\chi^2 = 1.13$, $p = 0.29$). As was observed among mothers and alloparents in general, subadults rarely initiated associations with offspring. We observed only one subadult that actively initiated an alloparental association with a focal offspring. This occurred when a subadult approached and briefly escorted a lone yearling that had swum several body lengths away from its mother. In all other focal follows, it was either not apparent which individual initiated the association ($N = 3$), or the association was initiated by the focal offspring ($N = 5$). We observed no alloparental associations between calves and subadults.

3.4. Impact of offspring age class on maternal investment

Results from the Association model, the Echelon model, and the Infant model and their associated Tukey tests show that offspring age impacted the duration of maternal behaviours, but not alloparental behaviours. Output from the models show how the levels of each fixed categorical variable and their interactions influenced the duration of behaviours, relative to the interaction between calf and mother, randomly chosen as the intercept (Table 6). Our models showed that calves with mothers had significantly longer associations ($z = -6.96$, $p < 0.001$) and escort swims ($z = 10.0$, $p < 0.0001$) than yearlings with mothers, and significantly longer associations ($z = -12.66$, $p < 0.001$) and escort swims ($z = -19.0$, $p < 0.001$), but shorter infant swims ($z = 3.62$, $p < 0.001$), than juveniles with mothers. Results from the Tukey test also showed that yearlings with mothers had significantly longer echelon swims than juveniles with mothers ($t = -3.07$, $p = 0.03$). We summed the model intercepts and relevant slopes to obtain estimates of

Table 6.
Association model, Echelon model, and Infant model describing the duration of offspring-care behaviours as a function of escort type (mother or alloparent) and offspring age class (calf, yearling, or juvenile) and their interaction.

Response variable	Model		
	Association	Echelon	Infant
	Duration of association (s)	Duration of echelon swim (s)	Duration of infant swim (s)
Fixed effects			
Intercept	103.6*	76.7*	12.6*
(Calf × Mother)	[94.9, 112.3]	[70.5, 83.0]	[9.5, 15.6]
Type: Alloparent	−78.8*	−53.2*	−10.8*
	[−94.0, −63.5]	[−64.2, −42.2]	[−15.6, −6.0]
Age: Yearling	−45.6*	−46.6*	4.2
	[−58.4, −32.8]	[−55.8, −37.3]	[−0.5, 9.0]
Age: Juvenile	−56.0*	−59.8*	5.9*
	[−64.8, −47.2]	[−66.1, −53.6]	[2.7, 9.1]
Yearling × Alloparent	31.5	28.1*	−3.6
	[−5.1, 68.2]	[4.0, 52.4]	[−15.8, 7.6]
Juvenile × Alloparent	43.8*	42.8*	−4.2
	[23.5, 64.1]	[28.9, 56.7]	[−10.1, 2.9]
Marginal R^2 (fixed effects only)	0.11	0.17	0.04
Conditional R^2 (fixed and random effects)	0.24	0.28	0.45

95% confidence intervals for each estimate included in brackets. Estimates accompanied by an asterisk (*) were statistically significant ($p < 0.05$).

the duration of each maternal behaviour (Figure 4A–C), and used results of the post-hoc tests to indicate whether differences between age classes were significant. Overall, maternal association and echelon swim duration decreased with offspring age (Figure 4A, B), while maternal infant swim duration increased with offspring age (Figure 4C).

3.5. Impact of offspring age class on alloparental investment

We also summed the model intercepts and relevant slopes to estimate the duration of all alloparental behaviours, and used the results of the Tukey post-hoc tests to determine whether differences between age classes were significant (Figure 4D–F). The large confidence intervals surrounding alloparental estimates reflect the high variability in behaviour duration observed

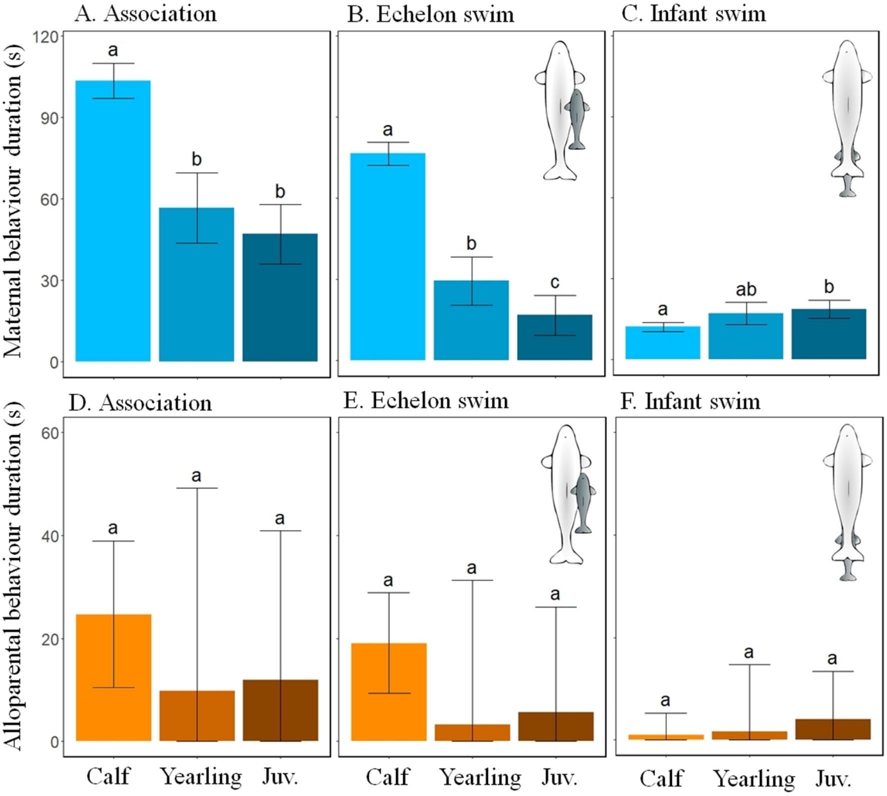

Figure 4. Estimates of the duration of maternal care behaviours (shades of blue, panels A, B, C) and allocare behaviours (shades of orange, panels D, E, F) calculated from the Association model (panels A, D), Echelon model (panels B, E), and the Infant model (C, F). Age classes sharing the same letter within the same panel were not significantly different, while age classes with different letters were significantly different ($p < 0.05$). Confidence intervals were bounded at zero, as our models did not specify that estimates must be positive. Age classes were only compared within, and not among, panels.

even within age class-escort type combinations. While the estimates for alloparental association duration and echelon swim duration for calves are noticeably greater than the estimates for yearlings and juveniles, all estimates were associated with very large confidence intervals, such that all differences observed across age classes were non-significant (Fig 4D–F). Since our maternal associations far outnumbered our alloparental associations, we considered that the lack of significance observed in the duration of alloparental associations might be an artifact of its small sample size. Therefore, we repeated the analysis using only the subset of focal follows that had both maternal ($N = 257$) and alloparental associations ($N = 257$). When maternal and alloparental associations both had identical sample sizes, we found no change in our results (data no shown).

4. Discussion

Using focal observations of beluga offspring in the St. Lawrence Estuary, we assessed whether the learning-to-parent and the natal attraction hypotheses are consistent with allocare in this population. Based on anecdotal observations of wild belugas (Bel'kovitch & Sh'ekotov, 1993), we hypothesized that beluga allocare is driven by natal attraction and learning-to-parent, as has been reported among bottlenose dolphins (Mann & Smuts, 1998). However, our results suggest that the learning-to-parent and natal attraction hypotheses are unlikely candidates to explain to occurrence of allocare in this beluga population. We found that subadult alloparents provided care no more frequently than expected, and that subadults rarely initiated allocare. Indeed, most maternal and alloparental associations were initiated by offspring, suggesting that offspring sought out associations with escorts, rather than escorts seeking out associations with offspring. We also found that maternal investment tended to decline as offspring aged, as shown by a decrease in maternal association and echelon swim duration, coupled with an increase in the duration of infant swims. However, alloparental investment did not vary with offspring age. Neither the duration of alloparental associations, echelon swims, or infant swims varied significantly with offspring age class. In sum, our results show that allocare in SLE belugas is likely inconsistent with the learning-to-parent and natal attraction hypotheses.

4.1. Patterns of maternal investment

The observed patterns of maternal investment showed that, as offspring aged, mothers spent less time in association with offspring, and replaced high-cost maternal behaviours with lower cost behaviours. A similar pattern of declining maternal investment is apparent in belugas of the eastern Canadian Arctic that show gradual weaning, with offspring diet progressively shifting from exclusively milk, to exclusively solid foods across a multi-year timespan (Matthews & Ferguson, 2015). Studies of captive belugas also corroborate this trend, as calves tend to become less dependent on their mothers over the course of their first year (Hill, 2009; Hill et al. 2013). Maternal investment, defined by the same metrics used in our study, also showed a similar decline among the bottlenose dolphins of Shark Bay. In this population, offspring gradually spent less time in association with their mothers as they aged (Stanton et al., 2011), and the predominant behaviour of mother-offspring dyads shifted from echelon position to infant position (Mann & Smuts, 1999; Noren & Edwards, 2011). This confirms that the metrics used to measure alloparental investment accurately captured variation in maternal investment across age classes.

4.2. The learning-to-parent hypothesis

Through the learning-to-parent hypothesis, allocare has been suggested to improve direct fitness of alloparents, by allowing young females to acquire infant-handling experience before producing their own offspring (Lancaster, 1971). If allocare in the SLE beluga population persists as a low-risk parenting exercise, we predicted that subadult females would be over-represented among alloparents, and that alloparental investment would decline as offspring aged. We found little support for the learning-to-parent hypothesis. Subadult alloparents were observed no more frequently than expected, and subadults generally showed little interest in associating with offspring. In addition, alloparental investment did not decline with offspring age, and subadults never associated with calves. These results contrast with reports of subadult-tended 'kindergarten groups' among White Sea belugas (Bel'kovitch & Sh'ekotov, 1993), and observations of allocare in bottlenose dolphins, where immature females frequently attempt to separate newborn calves from their mothers to engage in echelon swims (Mann & Smuts, 1998). Among primates, the learning-to-parent hypothesis tends to receive strong support. Across taxa, juvenile and subadult females interact with offspring more than non-parent adults (Maestripieri, 1994). For example, among ursine colobus (*Colobus vellerosus*) subadult females carry both related and unrelated offspring for long periods of time (Brent et al., 2008; Bădescu et al., 2015).

4.3. The natal attraction hypothesis

Natal attraction, an indiscriminate attraction towards infantile traits perceived to be 'cute', has been suggested to be a major driver of parental and prosocial behaviours in group-living animals (Silk, 1999; Archer & Monton, 2011; Stark et al., 2016). We found little support for natal attraction as a driver of allocare in belugas. Alloparental investment did not vary significantly across age classes, inconsistent with the natal attraction hypothesis. In addition, we found that most alloparental associations were initiated by offspring rather than alloparents. Our observations align with reports of allocare in captive belugas, where calves were found to initiate most maternal and alloparental associations (Hill & Campbell, 2013). These findings support our conclusion that allocare in belugas is not driven by an indiscriminate attraction to infants. Despite being sometimes described as a 'reproductive error', natal attraction does not imply that animals are unable to recognize their own offspring, but rather that certain traits have been selected to elicit care-giving behaviours (Riedman, 1982; Silk, 1999). Immature females seem particularly sensitive to infantile traits, such that learning-to-parent allocare and natal attraction often occur in conjunction. Both immature bottlenose dolphins and ursine colobus females are most strongly attracted to infants (Mann & Smuts, 1999, Bădescu et al., 2015). Given that older offspring possess fewer infantile traits than infants, natal attraction typically ceases as offspring age (MacKinnon, 2011).

4.4. Untested hypotheses for the evolution of allocare

In this study, we tested the learning-to-parent and natal attraction hypotheses for the evolution of allocare, but allocare is also known to arise when alloparents gain an inclusive fitness benefit by caring for kin (kin selection; Trivers, 1972), when alloparents receive reciprocal allocare or other benefits by providing allocare (reciprocation; Trivers, 1971, 2006), or when the survival of offspring favours alloparents by increasing group size (group augmentation; Kokko et al. 2001). Among the sperm whales of the Caribbean and Sargasso seas, evidence suggests that allocare is driven by kin selection and reciprocation (Gero et al., 2009, 2013; Konrad et al., 2018). In these populations, adult alloparents preferentially care for closely related offspring, and in one case, reciprocation of allocare between two mothers was observed after a one-year delay (Gero et al., 2013). Similar patterns of allocare are seen in capped langurs (*Presbutis pileate*), where alloparents are almost exclusively adult, parous females, and allocare occurs primarily between kin and reciprocating females (Stanford, 1992). Among sperm whales, group augmentation might also drive the occurrence of allocare. Sperm whale females remain in their natal groups, so it may be advantageous for group members to help raise female offspring if larger social groups are beneficial (Konrad et al., 2018).

The group augmentation hypothesis seems implausible as a driver of allocare among belugas. Indeed, the stable group structure required by the group augmentation hypothesis (Kokko et al., 2001) is inconsistent with the fission-fusion social dynamics of belugas (Alekseeva et al., 2013). However, the kin selection and reciprocation hypotheses both appear consistent with beluga behaviour and social structure. Observations of high relatedness within female groups during migration suggests that female belugas may prefer to associate with kin (Colbeck et al., 2013). In addition, belugas are one of a few species with post-reproductive female lifespans (Ellis et al., 2018), which may suggest that grandmothers play a role as caregivers. Evidence from belugas kept in captivity suggests that kinship may be an important consideration during allocations of allocare. Indeed, Hill & Campbell (2014) suggest that belugas prefer related alloparents when kin are available, as evidenced by a female calf whose preferred alloparent was her half-sister. However, Leung et al. (2010) noted that a male beluga calf was allonursed by both his half-sister and an unrelated female, at times preferring the unrelated female. Other findings also suggest that beluga sociality is not exclusively structured by kinship: O'Corry-Crowe et al. (2020) found that all beluga groups examined included both related and unrelated individuals, and that most groups tended to have low relatedness. This suggests that long-term bonds among belugas, rather than being exclusively shaped by kinship, might also result from cooperative behaviour.

4.5. Possible benefits of 'extended' allocare

Our observations that beluga allocare did not vary significantly across age classes requires further inquiry but suggests that allocare might be important for older offspring. In some species, offspring benefit from 'extended' allocare. Among capuchins, constant levels of allocare are maintained as offspring age, such that older offspring receive more allocare than maternal care (O'Brien & Robinson, 1991). Such extended allocare likely benefits both mothers and offspring. By seeking out associations with alloparents, offspring may acquire social skills and develop strong bonds within their social network. Several studies have shown that early connectivity in social networks can lead to improved outcomes for offspring (McDonald, 2007; Nunez et al., 2015). Mothers likely also benefit from extended allocare. When relieved of maternal care duties, even briefly, mothers might be able to increase their investment in future reproduction. In species with high levels of allocare, offspring tend to grow rapidly and wean at an early age (Ross & MacLarnon, 2000). Among vervet monkeys (*Chlorocebus pygerythrus*), mothers that received assistance from alloparents had shorter birth intervals than mothers who reared their offspring alone (Fairbanks, 1990). By investing in older offspring as well as in infants, beluga alloparents may provide relief to mothers at a time when maternal care becomes particularly costly. Further investigation is needed to confirm whether our observed patterns of allocare reflect extended allocare, and whether the role of alloparents changes as offspring age.

4.6. Study limitations

In this study, we were unable to genetically identify mother-offspring relationships. We operated under the assumption that a focal offspring's 'main adult escort', the adult female with whom the offspring spent most of a focal follow, was its mother. However, during shorter focal follows it is possible that we misidentified alloparents as mothers, or mothers as alloparents. While we validated our assumptions for a single highly recognizable mother-offspring pair, this single case does not imply that our definitions correctly identified all mothers. Due to limited knowledge of the occurrence of allocare among wild belugas, we attempted to be conservative in defining alloparents. Patterns of allocare in wild belugas should be further examined with marked individuals to determine whether our assumptions were valid.

4.7. Conclusion

From observations of alloparental associations in the SLE beluga population, we found that alloparental investment remained constant across age classes and that most alloparental associations were initiated by offspring, inconsistent with the natal attraction and learning-to-parent hypotheses. Subadult alloparents were not over-represented, and showed little interest in offspring, further discounting the learning-to-parent hypothesis. While we were unable to test the kin selection and reciprocation hypotheses, these two hypotheses for the evolution of allocare are both relevant to the behavioural ecology of wild belugas. Future work should focus on disentangling how relationships between kin and non-kin impact the expression of cooperative behaviours among belugas. In sum, allocare among SLE belugas likely arises from cooperation between kin and unrelated social partners, but not as a means of gaining parenting experience, nor due to an innate attraction to infants.

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Appendix A: Frequency of re-observation of known individuals

Since 1985, the Groupe de Recherche et d'Éducation sur les Mammifères Marins (GREMM) has lead an extensive effort to photograph and catalogue SLE belugas. Over hundreds of cumulative hours, the GREMM's researchers have followed herds of belugas and attempted to photograph all individuals encountered. The photographs are then scrutinized to identify persistent scars, discolorations, and malformations, and matched to previous photographs of the same animal. Known animals are issued an alphanumeric code and re-observed year to year. To date, the GREMM has successfully catalogued several hundred animals, approximately 15–20% of the total population (R. Michaud, unpublished data).

As our UAV footage was not optimized to allow individual recognition of animals, we did not have a good estimate of the true number of animals

Table A1.
Results of photo-identification effort over the course of the 2016–2018 field seasons.

	2016	2017	2018
Sampling days	28	19	30
Known individuals	36	22	29
Mean number of sampling days observed (± SD)	2.6 ± 2.2	2.5 ± 1.5	2.4 ± 1.6
Within-season recurring individuals	21	15	16
Re-observation interval of within-season recurring individuals (± SD)	Every 6.2 sampling days ± 4.6	Every 5.8 sampling days ± 4.1	Every 6.3 sampling days ± 5.3

For individuals that were observed in multiple years, each year's observations were tabulated separately. Within-season recurring individuals refers to animals that were observed on more than one sampling day within a field season.

sampled. Over our 2016, 2017 and 2018 field seasons, we observed belugas over 69 sampling days. The observed herds numbered, on average, 26.3 individuals with a standard deviation of 16.3, and ranged in size from 1 to 80 individuals. To ensure that we were not always observing the same small subset of the population, we calculated the frequency of re-observation of photo-identified individuals. Photoidentification protocols were carried out in our study site over 77 sampling days from 2016 to 2018.

In total, we observed 60 known individuals in the study area during the 2016–2018 field seasons. Most known individuals were only observed on a few sampling days each season (Table A1). For individuals that were observed on multiple days within a season (i.e., recurring individuals), we found that most individuals did not remain in the area for several days, but rather left the area and only returned after several days of absence (Table A1).

Our findings support the notion that the study area is frequented by a well-mixed subset of the population. None of the known individuals were consistently re-observed on every sampling day of any field season. In 2018, one known individual was re-observed on five sequential sampling days, but this was unusual. Most known individuals were only observed a few times per field season. For known animals that were observed more than once in a field season, patterns of re-observation suggest that most animals do not remain in the study area or return consistently for several days at a time. This has implications for the true sample size of this study. While it is inevitable that certain focal individuals were resampled, our findings do not suggest that every sampling day consisted of resampling the same mothers and offspring.

Appendix B: Interobserver analysis

To ensure the reliability of the main observer (JAA), we trained two additional observers (BJ and AKE) to re-analyse a subset of the videos using the event recorder JWatcher 1.0 (Blumstein & Daniel, 2007). We re-analysed 28 videos from a total of 179. BJ and AKE analysed 11 and 17 videos, respectively (Table 4). These videos were randomly selected across all sampling seasons. JWatcher's "Analysis" function was used to summarize the observer's observations and produce files that we imported into the R environment (version 3.4.3, R. Core Team, 2013) for further analysis. As we were only interested in assessing JAA's reliability, we pooled the observations of the two observers. As the videos contained multiple overlapping focal follows, we were unable to compare observations by focal follow. Instead, we summed all behaviour durations and counts of interest within a video and compared all variables by video. We used the intraclass correlation coefficient with a two-way mixed effects model to assess the reliability of JAA's observations using the ICC function of the psych package (Revelle, 2018) in the R environment (version 3.4.3, R. Core Team, 2013). We reported the results for type ICC3K, as we were not interested in generalizing our findings to a population of observers, and we estimated reliability for an average of several observations (Table 4).

Following Koo & Li (2016), we considered that an intraclass correlation coefficient from 0 to 0.5 showed poor agreement between the observers, 0.5 to 0.75 showed moderate agreement, 0.75 to 0.9 showed good agreement, and 0.9 to 1.0 showed excellent agreement. For the 28 videos analysed, all variables of interest showed moderate to excellent agreement between JAA and the two observers.