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Characterizing alloparental care in the pilot whale (*Globicephala melas*) population that summers off Cape Breton, Nova Scotia, Canada

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ABSTRACT

Alloparental care happens when a calf is cared for by an adult that is not their parent. Although alloparental care is common in social mammals, its prevalence is difficult to assess in cetaceans, and has not been studied in *Globicephala melas*. A population off Cape Breton, Nova Scotia, has been studied from whale-watching vessels since 1998, during July and August each year. From 2009 to 2011, we collected photo identifications of calves and the adults accompanying them. Alloparental care was considered to be occurring when a calf was identified with more than one companion. We found that 85.7% of calves in 2009, 80.6% of calves in 2010 and 63% of calves in 2011 had alloparents. Mothers were difficult to identify. Nevertheless, none of the other companions of calves were assigned to the same unit as the mother. Five carers were sexed, four of them males. There were no cases of within- or between-year alloparental care reciprocity. It is possible that delayed reciprocity is happening on a larger time scale in this population, but the most likely explanation is that alloparental care is a byproduct of this species' social structure, with a very small cost to the alloparent's fitness.

Key words: alloparental care, pilot whale, *Globicephala melas*, social structure, behavior.

In mammals, the care of young is mostly provided by the mothers (Kleiman and Malcolm 1981), but in some species others may also help: fathers, siblings, or even unrelated individuals (Kleiman and Malcolm 1981, Riedman 1982, Jennions and MacDonald 1994, Woodroffe and Vincent 1994). These are considered *alloparents*. Alloparental care can be defined as any nonparent taking part in the process of raising young, by engaging in behaviors that benefit the young (Woodroffe and Vincent 1994). Alloparental care is linked to group living and sociality (*e.g.*, Konig 1997). It is often used as a synonym of cooperative breeding (Fernandez-Duque *et al.* 2009), although cooperative breeding can be defined more strictly as a proportion of females in the group not reproducing regularly, and instead helping to care for the young of others (Boomsma 2007, Cornwallis *et al.* 2010, Lukas and Clutton-Brock 2012).

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Alloparental care can be divided into two forms, direct and indirect (Kleiman and Malcolm 1981). In direct parental care there is an interaction with the young, such as grooming, huddling, or providing food, which can increase the probability of survival of the young. When the behavior is not directed towards the young, but still influences its survival, it is considered indirect alloparental care, for example shelter construction and maintenance, or sentinel behavior (Kleiman and Malcolm 1981).

Babysitting is a particular case of direct alloparental care, where the carer purposefully changes its behavior to stay close to the young to its benefit (Whitehead 1996). For example, meerkat (*Suricata suricatta*) pups are babysat in their natal burrow, while mothers leave the colony to forage with other members of their group. Each nursery has one or two babysitters that stay behind to care for the babies. While the babysitters are caring for the babies, they usually do not eat, and may lose up to 2% body weight during the babysitting day. If, instead of babysitting, individuals were foraging they would be able to maintain, or even gain, body weight (Clutton-Brock *et al.* 2001). Costs of behavior are not always this high with all species. For instance, sperm whales (*Physeter macrocephalus*) babysit by changing their dive synchrony and take care of the calf at the surface, which likely has a very small cost (Whitehead 1996).

For alloparental care to happen, the costs for the alloparent need to be balanced by its benefits. When costs are negligible, alloparental care can be a byproduct of the evolution of sociality. Indirect alloparental care and communal broods or colonies will often fit into this category. When alloparental care is costly, it has to be maintained by an adaptive mechanism. These mechanisms can be divided into two different types of systems: *investment*, where the alloparents' rewards are based on the behavior of the young they helped previously when the young reaches maturity; and *signaling*, where alloparental care is performed for other individuals in the population to know about (Wright 1997, 1999).

Investment mechanisms include reciprocal altruism, kin selection, and group augmentation. Reciprocal altruism happens when the alloparent performs a beneficial action to another individual, which is detrimental to its fitness, with the expectation that it will be reciprocated (Trivers 1971, Axelrod and Hamilton 1981). Reciprocation does not have to be instantaneous, if individual recognition mechanisms are in place. Kin selection occurs when the alloparent helps its kin, in the expectation that it will help to increase the possibility to pass on their commonly-held genes to subsequent generations (Hamilton 1964*a*, *b*). In group augmentation alloparents help young, even if unrelated, with the expectation that they will stay in the group, increasing or maintaining the benefits of living in a large, well-functioning group (Brown 1987, Kokko *et al.* 2001). Signaling systems include pay to stay and social prestige. In pay to stay subordinate alloparents assist the dominant breeding pair as a way to *pay rent* to stay in the group (Gaston 1978, Kokko *et al.* 2002). In social prestige males care for young other than their own as a way to advertise their mating quality (Zahavi 1975, 1995).

Several cetacean species are known or suspected to engage in alloparental care. Bottlenose dolphins (*Tursiops* spp., Caldwell and Caldwell 1966, Mann and Smuts 1998) and killer whales (*Orcinus orca*, Bigg *et al.* 1987) are known to escort calves, a form of babysitting; sperm whales also babysit (Whitehead 1996, Gero *et al.* 2009); and sperm whales and beluga whales (*Delphinapterus leucas*) allonurse, *i.e.*, nurse calves that are not their own (Best *et al.* 1984, Leung *et al.* 2010). All these species live in social groups, of different types including labile fission-fusion and stable matrilineal units, as well as combinations of these elements (Rendell and Gero 2014).

Long-finned pilot whales (*Globicephala melas*) live in social units that coalesce to form ephemeral groups (Ottensmeyer and Whitehead 2003, de Stephanis *et al.* 2008), but little more is known about their social dynamics. Genetic studies on groups of pilot whales driven ashore in the Faeroe Islands, "grinds," found that the large groups that compose the grinds contain individuals of both sexes, but none of the males are the fathers of the calves in the same grind (Amos *et al.* 1991, 1993). Unfortunately, these studies do not give us information on how associations between individuals change over time. The Cape Breton, Canada (Ottensmeyer and Whitehead 2003) and Strait of Gibraltar (de Stephanis *et al.* 2008) populations show the above mentioned social structure of stable social units. The Strait of Gibraltar units are comprised of males and females (de Stephanis *et al.* 2008), while molecular sexing had not been performed in the Cape Breton population until this study (Ottensmeyer and Whitehead 2003). It has been hypothesized that units correspond to extended matrilines (Ottensmeyer and Whitehead 2003).

We examined patterns of escorting, *i.e.,* accompanying calves, and investigated several hypotheses, including: whether it is possible to identify who the likely mothers of the calves are due to their predominant accompaniment of the calf, given that in other cetacean species where alloparental care happens calves still spend a much larger amount of time with their mothers when compared to other carers; that given this species' cohesive social structure accompaniment of the calf by nonmothers, *i.e.,* alloparental care, happens at all developmental stages of the calf; and that alloparents are predominantly females in the same unit as the mother, which would allow for reciprocity of the behavior, as well as perhaps kin selection, driving the alloparental care.

METHODS

Data Collection

Data were collected in July and August, from 2009 to 2011 from a 13 m whale watching vessel off the northwest coast of Cape Breton Island, Nova Scotia, Canada. Up to five trips were conducted daily, departing from Pleasant Bay Harbor (46°49′N, 60°47′W) and lasting a maximum of 2.5 h each, covering up to 40 km south to 30 km north of the harbor, and a maximum of 8 km offshore. Trips were only performed when the wind strength was <20 knots.

Usually, two researchers collected behavioral and photographic data on each trip. In the rare case where only one researcher was available, priority was given to photographic coverage. The area was scanned for the presence of pilot whales, and when a group was sighted the vessel approached it slowly and kept parallel to their movement or stayed stationary with the motor on idle or turned off.

Data were collected and organized by encounters. Encounters began when a whale was sighted and ended when the vessel left the group by either returning to port or by moving to another group that was more than 200 m away. Encounters also ended if the group was submerged for more than ten consecutive min. All individuals in an encounter were considered to be in the same group. Calves were counted and photographed. Adults escorting them—closest companions—were also photographed, so they could be identified later. Escorting is defined as accompanying the calf in close proximity, <1 calf body length, while at the surface. Only one animal could escort a calf at any time. When several individuals are close to the calf, the one that surfaced within the least amount of time to the calf was considered the escort.

Tissue from adult individuals was collected by remote biopsy sampling in July and August 2010–2012, off the Pleasant Bay Harbor, from a semirigid 4.5 m inflatable zodiac, as in Kowarski *et al.* (2014).

Identification of Closest Companions

Closest companions were identified through pictures of the dorsal fin area (Auger-Méthé and Whitehead 2007). These were collected using a Canon 30D digital camera with a 200 mm or 300 mm autofocus lens. Each photograph was quality rated (Q) from 1 to 5 according to the attributes of focus, size, orientation, exposure, and percentage of fin visible. Individuals were identified using the number and position of mark points (MP), *i.e.*, nicks and internal corners of notches, of dorsal fins (Ottensmeyer and Whitehead 2003, Auger-Méthé and Whitehead 2007). Photo identification within each year was performed by eye by JFA on photographs with $Q > 2$ showing dorsal fins with $MP > 2$. Individuals with less than three MPs were deemed unidentifiable. Identifiable CCs were numbered within in each year using a year specific code (*e.g.*, 2009_a1, 2011_a3), matched between years and identified in the project catalog (identification numbers: *e.g.*, 235, 580) using Finscan (Araabi *et al.* 2000). In cases where we did not find a match for the adults in the project catalog they remained identified with their within-year number (*e.g.*, 2009_a1, 2011_a3). When one of those adults was identified in several years, the identifying number of its first year was used (*e.g.*, 680, in both 2009 and 2011).

Identification of Calves

Calves were identified individually (*e.g.*, c100, c70) using several different types of markings: pigmentation patterns, including the saddle patch and fetal folds, linear marks, tooth rakes, patches, white scars (Auger-Méthé and Whitehead 2007) and, when existing, MPs in the trailing edge of the dorsal fin (Ottensmeyer and Whitehead 2003; Auger-Méthé and Whitehead 2007). MPs and white scars are the only markings that remain constant with time (Auger-Méthé and Whitehead 2003). How clearly saddle patches can be observed increases with age and size of the individual (Bloch *et al.* 1993), but saddle patches do not disappear with time. The light coloration of calves and juveniles may make it harder to identify the saddle patch in animals of these age classes. The loss rate for the remaining markings (fetal folds, linear marks, tooth rakes, and patches) varies between 0.4/yr and 1/yr (Auger-Méthé and Whitehead 2003). Since the field season lasts 2 mo at the same time each year, and most of the markings used to identify individuals last less than a year, identifications were only possible within the field seasons, not between different field seasons, except for those individuals with three or more MPs in the dorsal fin or other markings that remained unchanged. Calves with one or more MPs on their dorsal fin or body could be identified between seasons. MPs are rare in calves, so it should be possible to identify individuals with a low number of MPs.

Calves were classified according to their age and morphology. Newborn calves have fetal folds and a bent over dorsal fin. Calves with fetal folds are younger than 1 yr. Gray calves are older than 1 yr, are gray, and have lost their fetal folds (Fig 1; Slooten and Dawson 1988, Herzing 1997, Grellier *et al.* 2003, Auger-Méthé and Whitehead 2007).

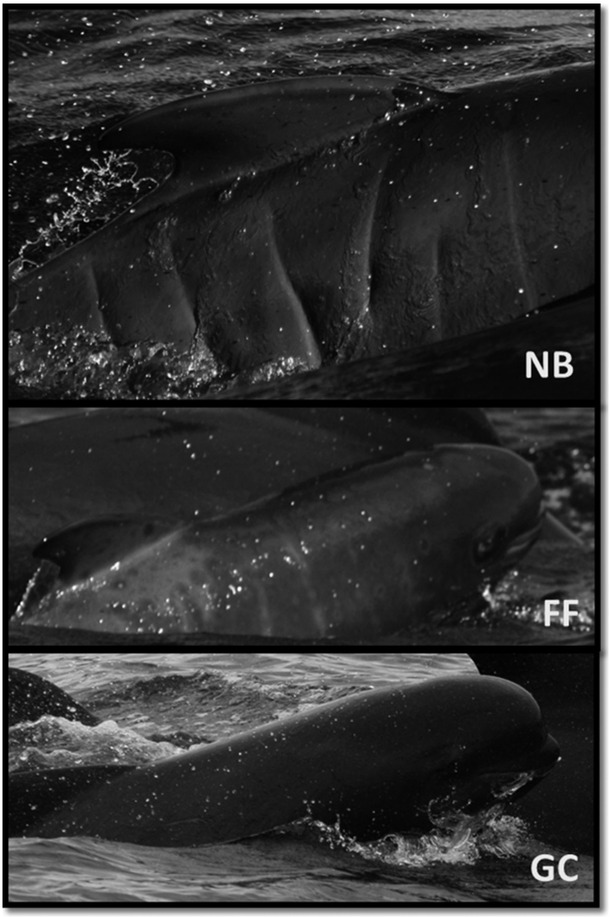

Figure 1. Identification of calf age using photography. NB = newborn, FF = fetal fold, GC = gray calf.

Characterizing Alloparental Care

Only calves that were identified in at least two encounters with identifiable CCs were included in the analysis. Instances of alloparental care happened when one calf was identified with more than one CC during the sampling period. Here, the assumption is that the observed close association is representative of alloparental care, even if specific care-giving behavior was not observed.

We assumed that the CC predominantly associated with a calf was its mother (see Grellier *et al.* (2003) for justification). When a calf was only observed with one CC, it was considered its mother. When calves were seen with multiple CCs we used an adaptation of the method described in Grellier *et al.* (2003) to assign the mother. We used the photographic records to calculate the coefficients of association between calves and CCs using the simple ratio index

$$SI = \frac{x}{n}$$

where x is the number of frames the calf and the CC were identified in the same, or consecutive photographs in the same surfacing event, and n the total number of frames either the calf or the CC were identified.

We then used a one tailed z-test to compare the CC with the highest SI for each calf (SI_1) and the CC with the second highest SI (SI_2)

$$z = \frac{SI_1 - SI_2}{\sqrt{SI(1 - SI)\left(\frac{1}{n_1} + \frac{1}{n_2}\right)}}$$

where $SI_1 = \frac{x_1}{n_1}$, $SI_2 = \frac{x_2}{n_2}$, and $SI = \frac{(x_1+x_2)}{(n_1+n_2)}$. This approach is only considered good when $n_1 + n_2 > 12$.The null hypothesis for this test is that the SIs are similar between the two CCs. When $z < z_{0.05}$ the null hypothesis is accepted, which means both CCs spent a similar amount of time with the calf. In this case, the maternity of the calf remains undetermined. When $z \geq z_{0.05}$ the null hypothesis is rejected, which means individual 1 spent more time with the calf. In this case, individual 1 is considered the mother of the calf. This method is only applicable when the mother has enough mark points to be identifiable.

We did not apply this method when the calf was seen in more frames with unidentified CCs than with identified CCs. Since mothers tend to spend much more time with the calf than alloparents (Whitehead 1996, Grellier *et al.* 2003) it was possible that the mother was an unidentified CC.

Reciprocal alloparental care happens when two mothers care for each other's calves. To determine whether this occurred within the population we determined which mothers cared for other calves, and who the mothers of those calves were. This analysis was performed within and between years.

Characterizing Alloparents

We characterized alloparents according to two characteristics, whether they were members of the same unit as the calves they were escorting and their sex. We defined units as sets of individuals in nearly permanent mutual association, comprised of key individuals and their close companions. Unit membership was assessed using a modification of the method employed by Christal *et al.* (1998) and Ottensmeyer and Whitehead (2003). Key individuals were those identified in at least four sampling days, with these days separated by at least 30 d. Close companions were those identified on the same day as key individuals, for at least three sampling days, and with sightings separated by at least 30 d. Calves were assumed to be in the same unit as their mothers.

To determine the sex of individuals we used molecular methods. DNA was extracted using the phenol:chloroform extraction method (Sambrook and Russel 2001). Sex of individuals was determined using a multiplex PCR of two primer pairs: one that amplifies a ~400 bp portion of the ZFX/ZFY gene (present on both sex chromosomes) and one that amplifies a ~200 bp portion of the SRY gene (only on the Y-chromosome) (Gilson *et al.* 1998). PCR was performed on 20 ng of purified DNA in a 20 μL reaction volume that contained 1X Taq polymerase PCR buffer, 0.2 mM dNTP, 1.5 mM $MgCl_2$, 0.3 μM of each primer, 0.16 mg/mL BSA, and 0.05 U/μL

Taq polymerase. PCR cycles were performed as follows: the first cycle at 94°C for 5 min, followed by 30 cycles of denaturation at 94°C for 30 s, annealing at 55°C for 1 min, and extension at 72°C for 1 min. A final extension step was performed at 60°C for 45 min. The PCR products were then separated and visualized using agarose gel electrophoresis in 1.5% agarose gels stained with ethidium bromide.

Results

Data Collection

Data were collected in a total of 661 encounters of pilot whale groups, 85.9% of which contained calves. In 2009 there were 239 encounters, 87.0% with calves; in 2010 there were 245 encounters, 86.9% with calves; and in 2011 there were 177 encounters, 83.1% with calves.

Identification of Calves and Closest Companions

A total of 356 calves were identified with MP > 2 between 2009 and 2011 (Table 1). Gray calves were more common than calves with fetal folds, and only one newborn was identified. Ninety-two calves were identified with more than one CC in two encounters and considered for the alloparental care analysis. This comprised 50% of all calves identified in 2009, 28% in 2010, and 18% in 2011 (Table 1). Two calves from 2010, c24 and c106, were removed from the maternity analysis due to a high number of identification efforts with CC that were not successful. A total of 90 calves were used for the following analyses.

Characterizing Alloparental Care

The number of CCs in relation to the developmental stage of the calves was not very variable. In 2009 and 2010, calves with fetal folds and gray calves both had a median of two CCs. Calves with fetal folds had between one and four CCs. In 2009, gray calves had between one and five CCs, and between one and four in 2010. In 2011 calves with fetal folds had a median of three CCs and grey calves of one CC.

Table 1. Summary of calf types identified in 2009, 2010, and 2011. Calves "Analyzed" refers to calves seen in more than one encounter with an identifiable CC, therefore able to be used in this study.

	Year	2009	2010	2011
Identified	Newborns	1	0	0
	Fetal folds	17	16	30
	Gray calves	38	113	141
	Total	56	129	171
Analyzed	Newborns	1	0	0
	Fetal folds	10	5	10
	Gray calves	17	29	20
	Total	28	34	30

Some calves were identified with only one CC: 14.3% in 2009, 19.4% in 2010, and 36.7% in 2011 (Table S1). There is a weak but positive relationship between the number of encounters in which a calf was identified and the number of identified CCs (Table 2, Spearman's rho: 0.242) While most calves were identified with more than one CC, there were several cases where only one CC was identifiable, so no further analysis were conducted.

There were apparent discrepancies in some results. In 2009 individual 1245, which is a male, was the only identifiable individual identified with calf c33. Also in 2009, individual 1353, another male, was identified as the individual that spent most time with both calves c18 and c20. Finally, in 2011 individual 717 was identified as the mother of two calves, c293 and c232.

The Grellier *et al.* (2003) method assigned mothers in three cases in 2009, one case in 2010, and four cases in 2011 (Table 3). There were 12 cases in 2009 and 2011, and 14 cases in 2010 where there were too few resightings for the method to be useful.

Twenty-one adults were seen escorting calves in multiple years (Tables 4 and S2). The calf "Patch" was consistently identified throughout the three years with the same adult, 2009_a2, and with her more frequently than other CCs, so we considered her its mother. Two adults were assigned as mothers during several years. Adult 2009_a101 was assigned as mother to calf c46 in 2009 and to calf c397 in 2011; adult 595 was assigned as mother to calf c90 in 2010 and c231 in 2010. Unfortunately, the calves were identified using different sides of their dorsal fins in different years, and presented no MPs, so matching them was not possible.

No instances of reciprocal alloparental care within or between years were found (Table S3). Three adults identified as mothers escorted calves of other mothers. Adult 1438 escorted the calf of 1379, which escorted the calf of an unidentified mother. Adult 2011_a25 escorted the calf of 2009_a10, which escorted the calf of 595. Adult 595 was not observed to escort any calf other than its own.

Characterizing Alloparents

There were only two cases where calves were seen with multiple CCs assigned to a unit. Neither of these belong to the same social unit. Calf c78 had CCs from units Q and K, L, N and U; and calf c143 had CCs in units K and H (Table 5).

A total of 75 adults were sexed, 32 females and 43 males, but only five of these were identified as CCs. From these five CCs, four were males and one a female. None

Table 2. Number of calves in relation to number of encounters and number of CCs they were identified with. Data set for 2009–2011 with only identifiable CCs accounted for.

Number of encounters each calf was identified in	Number of CCs each calf was seen with					Total number of calves per encounter	Mean number of CCs per encounter
	1	2	3	4	5		
2	23	32	8	1	0	64	1.8
3	6	3	7	0	1	17	2.24
4	1	0	4	2	0	7	3
5	0	0	1	0	0	1	3
6	3	0	0	1	0	4	1.75
11	0	1	0	0	0	1	2
Total	33	36	20	4	1	94	

Table 3. Maternity test adapted from Grellier *et al.* (2003) for 2009, 2010, and 2011. Significant test results are marked in bold ($z_{0.05}$ = 1.64). A1 High: CC with the highest simple ratio index (SI_1) with the calf; A2 High, CC with the second highest simple ratio index with the calf; $n1$, total number of times A1 High and calf were seen together; $n2$, total number of times A2 High and calf were seen together; z, unicaudal z-test result. Only cases with enough resightings to apply the method are shown.

Calf	A1 High	SI_1	A2 High	SI_2	$n_1 + n_2$	z
2009						
c15	**1550**	0.62	113	0.17	39	**2.86**
c23	**2009_a61**	0.73	1075	0.2	30	**2.93**
c8	**474**	0.67	1570	0.14	16	**2.1**
Patch	2009_a1	0.58	2009_a2	0.42	48	1.15
c14	861	0.31	1034	0.23	26	0.34
c24	1525	0.57	575	0.29	14	1.08
C28	517	0.5	2009_a79	0.5	16	0
c6	1448	0.43	1347	0.29	14	0.56
2010						
c128	**1283**	1	2010_a40	0.08	18	**3.76**
c89	2010_a12	0.25	312	0.11	13	0.64
c97	1438	0.28	2009_a61	0.27	29	0.03
c143	312	0.36	2010_a40	0.17	23	1.07
c153	312	0.25	2010_a23	0.25	16	0
c154	2009_a81	0.33	2009_a106	0.14	17	0.79
c184	2010_a43	0.4	2010_a20	0.38	13	0.09
2011						
c386	**2011_a25**	0.71	2009_a81	0.07	22	**3.18**
c387	**2009_a101**	0.5	2009_a81	0.14	20	**1.69**
c213	**2011_a53**	0.71	1050	0.14	14	**2.16**
c222	**1379**	0.67	2010_a2	0.18	20	**2.2**
c284	1161	0.5	113	0.5	16	0

of these CCs accompanied the same calf, so genetic relatedness between the mother and CCs, or among CCs, could not be assessed (Table 5).

Discussion

Methodological Limitations

There are several methodological limitations to be considered in this study. The first one lies with the identification of calves. While with adults we use MPs to identify individuals, calves rarely possess these types of marks (Auger-Méthé and Whitehead 2007). MPs can be gained by injuries (Sergeant 1962, Bigg *et al.* 1987), interacting with other individuals, predators, boats, or fishing gear. Pilot whale calves are born with unmarked or with very small marks on their fins. This means that for most calves we have to use other, more temporary, markers to identify individuals. Marks can be found on both dorsal fin and body (Auger-Méthé and Whitehead 2007), but are usually restricted to one side of the individual. This makes it harder to identify both sides of a calf, and to identify it over several years. This unfortunately hampers our ability to look at multi-year alloparental care patterns for this population.

Table 4. Closest companions identified in several years, and in which role they were identified in. CM = confirmed mother, CC = closest companion (when mother was not confirmed), or A = alloparent (CC when the mother is known as another individual).

Adult ID	Calf id in 2009	Role	Calf id in 2010	Role	Calf id in 2011	Role
2009_a2	Patch	CC	Patch	CC	Patch	CC
2009_a28	c12	CC	c229	CC	—	
113	c14	A	—	—	c284	A
	c15	A				
1086	c14	A	c162	CC	—	—
	c15	A	c163	CC		
2009_a45	c18	CC	c69	CC	—	—
808	c20	CC	c143	A	—	—
228	c21	**CM**	c61	CC	—	—
2009_a61	c23	**CM**	c97	CC	—	—
575	c24	CC	—		Patch	CC
517	c28	CC	c76	CC	—	—
2009_a81	c31	CC	c154	CC	c239	**CM**
					c306	A
					c307	A
2009_a101	c46	**CM**	—	—	c307	**CM**
637	c47	CC	c132	CC	c266	CC
	c56	CC	c159	**CM**		
2009_a106	c48	CC	c126	CC	c268	CC
			c154	CC		
1283	c48	CC	c128	**CM**	—	—
1449	c6	CC	c178	CC	—	—
2010_a2	—	—	c57	CC	c216	CC
					c222	A
1455	—	—	c69	CC	c189	CC
1438	—	—	c88	CC	c311	CC
			c97	A	c222	A
			c98	**CM**		
595	—	—	c90	**CM**	c231	**CM**
1037	—	—	c131	CC	c131	CC

The second methodological issue is that the proportion of animals with MP > 2 is only about 0.34 for this population (Ottensmeyer and Whitehead 2003). While this proportion is enough for studying some aspects of social structure (Ottensmeyer and Whitehead 2003), it means that a large percentage of individuals escorting calves cannot be identified. These can be either mothers or companions. This is the case of the mother of calf c33, for instance. The only identifiable individual escorting calf c33 was individual 1245, which was a male. This presumably means the mother was an individual without enough MPs to be identified. There were also cases where individuals were not identified in the population catalog and remained with their within-year codes (*e.g.*, 2009_a2).

The third methodological issue is the low number of repeated observations of the companions with the same calf. There are several reasons for this. The study population is in the thousands. Data are collected from an opportunistic vessel, giving limited encounter durations. Also, groups are not often seen repeatedly on different trips on the same day. Likewise, the photographic data are difficult to collect for both calf

Table 5. Closest companions (CCs) that were affiliated with a unit or genetically sexed.

CC	Unit	Sex
261	K, L, N, U	
280	D	M
312	K	
517	O	
543	M	
602	Q	
637	O	
808	H	
861	U	
1162		F
1245		M
1353		M
1441		M

and companion simultaneously. The percentage of identified calves used in the study varies from 50% to 18% of calves over different years (Table 1). In many cases when we collected a Q > 2 picture of a calf, we did not also collect a Q > 2 photo of the companion, or *vice versa*. There is also a biological factor that might be influencing the low number of repeated observations of a particular individual accompanying a particular calf. With escorts and calves being members of the same group, but not necessarily of the same unit, and groups being ephemeral it might be that different individuals escort the same calf over time. With our opportunistic sampling strategy we might not be able to study the same group enough times to see repeated alloparental care events by the same individuals before the group breaks up.

Characterizing Alloparental Care

Given the limitations stated above, it was only possible to assign mothers to calves in a small number of cases. Grellier *et al.*'s (2003) method yielded results assigning mothers when more than one CC was present (Table 3), but for many cases there were not enough data for the analysis to be used reliably. But even with our methodological limitations it is possible to detect alloparental care.

We operationally defined alloparental care as taking place when a calf was being escorted (accompanying a calf at less than 1 calf body length, while at the surface) by only one individual, who was not the calf's mother. It was not straightforward to discriminate mothers from other escorts (CCs). However, in observations between 2009 and 2011, more than 50% of all calves identified were seen with more than one companion (Table 3), at least one of whom was not the mother. This constituted alloparental care according to our definition.

It is reasonable to assume that a calf is safer if accompanied by an adult than on its own. Hence, escorting should be considered alloparental care. This definition also aligns with those in some other species. For instance, in African elephants (*Loxodonta* spp.) individuals are considered caring when they greet and investigate calves, or when they provide assistance to a calf in distress (Lee 1987). In cetaceans, definitions are usually based on how close calves are to potential alloparents. With bottlenose dolphins, an individual is considered to be an alloparent if it is seen next to a calf (*e.g.*, Mann and Smutts 1998, Grellier *et al.* 2003). Similarly, with killer whales individuals are considered alloparents when they accompany calves (Bigg *et al.* 1990). With sperm whales, when mothers deep dive, the allocarer is the individual that stays close to the calf at the surface (Whitehead 1996).

Given that pilot whale social structure is built upon stable units (Ottensmeyer and Whitehead 2003, de Stephanis *et al.* 2008) this result is not unexpected. Members of other cetacean species that live in unit-focused societies, such as sperm whales and killer whales, are known to show alloparental care for each other's calves (Bigg *et al.* 1990, Gero *et al.* 2009). In sperm whales calves are even thought to be central to unit stability and alloparental care to be the primary function for units (Gero *et al.* 2013).

In our study, calves <1 yr old have roughly as many different escorts as calves >1 yr old. Due to the difficulties of finding enough markings on newborns to identify them, there are not enough data on newborn calves to test whether they are cared for by more or fewer individuals than older calves. Newborn calves are cared for by alloparents in other species. In sperm whales, for instance, there is alloparental care for calves when they are still newborns, <2 mo old (Gero *et al.* 2009). In meerkats alloparental care also occurs when pups are quite young. From their third week, pups are babysat by one or two alloparents in the natal burrow while the remainder of the group forages (Clutton-Brock *et al.* 1998).

Characterizing Alloparents

Given the strong associations between members of the same unit, we expected to find alloparental care preferentially happen within units. However, we found that alloparental care for a particular calf is being performed by individuals not in the same unit as each other or as the mother of the calf. In fact, we found no cases of individuals of the same unit caring for the same calf, so alloparental care is happening at the group level. Groups are much more ephemeral than units, lasting from hours to days (Ottensmeyer and Whitehead 2003). So, alloparental caring events should also be more ephemeral and with less opportunities for individuals to reciprocate.

Four out of the five sexed CCs were male, which indicates that male pilot whales perform alloparental care under our definition. This happens in some other species, such as killer whales (Bigg *et al.* 1990), bottlenose dolphins (Lusseau 2007), Atlantic spotted dolphins (*Stenella frontalis*, Weinpress and Herzing 2015), spectral tarsiers (*Tarsius tarsier*, Gursky 2000), and black snub-nosed monkeys (*Rhinopithecus bieti*, Xiang *et al.* 2010). Unlike killer whale males, which care for related calves within their own pod, male pilot whales are, at least sometimes, caring for calves outside of their units. In bottlenose dolphins, male alliances can escort females and young, which might be an alloparental caring strategy to prevent infanticide of their descendants (Lusseau 2007). In Atlantic spotted dolphins males discipline young, promoting behaviors more desired in group living, and hence their fitness (Weinpress and Herzing 2015). Spectral tarsier juvenile and adult males both groom and play with young (Xiang *et al.* 2010). In these last two cases it is possible that young are learning from their male carers how to behave socially. Social norms and behaviors are very important in group living. It is possible that male pilot whales are also providing important social experience for calves.

Why Does Alloparental Care Happen?

If escorting is costly—Showing alloparental care for another's calf can have costs for the alloparent, such as increased risk of predation by protecting the calf (*e.g.,* canids, Woodrof and Vincent 1994) and energy costs by decreasing foraging time (*e.g.*, meerkats, Clutton-Brock *et al.* 2000). If escorting is costly, there have to be evolutionary mechanisms in place for it to have evolved. Given that alloparental care is happening outside of units, it seems to preclude alloparental care being driven by kin selection (Hamilton 1964*a*, *b*). Given that groups are known to be ephemeral on a short time scale, separating in a matter of hours or days (Ottensmeyer and Whitehead 2003), group augmentation (Brown 1987) also seems an extremely unlikely mechanism to be acting in this population.

Reciprocal altruism (Trivers 1971) could be an explanation for alloparental caring behavior within groups. With altruistic interactions, an individual behaves in a way that is detrimental to itself, but beneficial to another. Altruism can evolve as a strategy due to the expectation that the selfless behavior will be reciprocated in the future—reciprocal altruism (Trivers 1971, Axelrod and Hamilton 1981). We did not find any cases of alloparental caring reciprocity either within or between years in this study. Given that we cannot identify all the mothers of the calves studied, reciprocity is hard to determine. But, in the two cases where we could follow two mothers and their calves across years (2009_a2 and 595) neither was observed to provide alloparental care for any other calf. Reciprocity may be occurring at a different time scale than our study can identify. Since alloparental care is happening within groups, which are ephemeral structures, it is possible that there are not many opportunities for individuals to reciprocate alloparental care within a small time scale. This reciprocity might only be happening when units congregate in groups after long periods of time. Also, it is possible that alloparental care is delayed until the calf is not dependent on its mother. We know that delayed reciprocity can happen with sperm whales (Gero *et al.* 2013) and African elephants (Lee 1987). Mothers might care for others during their interbirth interval or, possibly, after becoming reproductively senescent (Sergeant 1962). Given that there is no technique to age live pilot whales, the reproductive senescence hypothesis is currently impossible to test.

If alloparental care is mostly happening when escorting individuals do not have calves of their own, it is also possible that immature females also serve as carers. In this case reciprocity would not necessarily need to happen, since the females are gaining other benefits from alloparental caring, such as learning how to take care of young. It is hypothesized that this is the case with bottlenose dolphins (Mann and Smuts 1998) and with vervet monkeys (*Chlorocebus pygerythrus,* Fairbanks 1993).

It has been suggested that some male bottlenose dolphins in Doubtful Sound, New Zealand, continuously associate with new mothers and their offspring because they recognize calves as their own (Lusseau 2007). We know from Amos *et al.* (1991, 1993) that male pilot whales do not sire offspring in their "grinds," but due to the ephemeral natural of groups it is unlikely that male pilot whales find related calves for which to provide alloparental care in the different groups that they associate with. It is possible that males are providing alloparental care as a way to show their mating potential to females, a strategy known as social prestige (Zahavi 1975, 1995). According to this theory, males take on a *handicap*, *i.e.*, a costly behavior, as a way to advertise their mating potential to females. This handicap would be too expensive for a male with inferior mating potential to take. In this specific case, the handicap would be displaying the altruistic behavior of alloparental caring for calves that are not their offspring.

If escorting is not costly—There is no need for an evolutionary mechanism to be in play for it to emerge in the population. So, escorting would not be an altruistic act, but an act without cost to the individual's fitness. This could happen if the energetic and other requirements of escorting are negligible. In that case the individual would be able to behave in the same manner when escorting or not escorting a calf, or the differences would be negligible. This is supported by the ubiquity of alloparental caring events in our study. They do not appear to be associated with any particular behavior on the part of the carers, and carers do not seem to change their behavior during an event. These events are also not linked with any obvious costly behavior, such as food provisioning, which has an effect on individual fitness. Alloparental care in sperm whales, for instance, probably has a low cost since the individual only has to change dive synchrony, which likely has a low effect on its fitness (Whitehead 1996). We could not find a published case of alloparental care with no cost. What is probably happening in this population is that the cost of escorting is so low that it is negligible. This would also explain why males provide alloparental care outside of their natal unit. If escorting has little to no impact, either proximately or ultimately, on the fitness of the adults, males should not actively deter calves from approaching and being escorted by them. Calves may, for various proximate (*e.g.*, curiosity) and/or ultimate (*e.g.*, increased protection from predators) reasons be attracted to swimming next to a variety of adults, including males.

Conclusion—Alloparental care behavior happens frequently in the Cape Breton pilot whale population. Alloparental care is performed by individuals not in the same social unit as the mothers of the calves, and is also performed by males. Even though we did not find any cases of within or between year alloparental care reciprocity in this three year frame, we hypothesize it is possible that delayed reciprocity is happening on a larger time scale. It is more likely, though, that alloparental care by escorting calves has a negligible cost to the carer's fitness, so there is no evolutionary mechanism associated with the behavior, and alloparental care is a byproduct of this species' social structure.

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SUPPORTING INFORMATION

The following supporting information is available for this article online at http://onlinelibrary.wiley.com/doi/10.1111/mms.12377/suppinfo.

Table S1. Calves identified with only one CC in 2009, 2010 and 2011. Enc. = number of encounters the calf was identified with the CC. None of the CCs were sexed.

Table S2. Calves identified with several closest companions in 2009, 2010 and 2011. CC = closest companions, when accompanied by "+" at least one other unidentified individual was also seen, Enc. = number of encounters calves and CCs were identified in, Sex = sex of closest companion, Unit = social unit to which the closest companion belongs to, when in italics units belong to the K complex. Confirmed mothers are bolded and italicized.

Table S3. Reciprocity between known mothers of calves in 2009, 2010, and 2011. NI = not identified.