

Changes in subantarctic fur seal pups' activity budget and diving behaviours throughout the rearing period

C. Guinet, N. Servera, T. Deville, and G. Beauplet

Abstract: Time spent in the water and diving behaviour of subantarctic fur seals (*Arctocephalus tropicalis* (Gray, 1872)) at Amsterdam Island in the southern Indian Ocean were investigated using time–depth recorders throughout the pup-rearing period. The main finding of this study, contrary to the findings of previous studies conducted on other fur seal species, was the decrease in the mean daily amount of time spent in the water throughout the pup-rearing period. The decrease in the amount of time spent in the water by older individuals compared with younger ones is likely to be related to the reduction of the pups' energy expenditure with a decreasing provisioning rate by their mothers. No change in the number of dives or the amount of time dedicated to diving relative to the time spent in the water could be detected throughout the pup-rearing period. The mean maximum dive depth increased with pup age and decreased with pup mass, and maximum dive duration was also found to increase with pup age. The positive effect of pup size on dive rates was the only relationship suggesting that pups' growth performance may act positively on the ontogeny of their diving capabilities. The large interindividual variation in the amount of time spent in the water and in dive rates, and the absence of any clear relationship with pup mass and pup growth performance, suggest the existence of alternative strategies: either pups invest more energy in developing their swimming and diving abilities, to the detriment of the body fat stores, or reduce their activity level to enhance body fat stores to increase their postweaning survival rate.

Résumé : Le temps passé dans l'eau et le développement du comportement de plongée au cours de la période d'élevage des nouveau-nés chez les otaries à fourrure subantarctiques (*Arctocephalus tropicalis* (Gray, 1872)) ont été étudiés au moyen d'enregistreurs de plongées à l'île d'Amsterdam, dans le sud de l'Océan Indien. Le principal résultat de notre étude est l'observation de la diminution du temps moyen passé quotidiennement à l'eau en fonction de l'âge des petits. Ce résultat, contraire à celui trouvé chez d'autres espèces d'otaries, semble être la conséquence de la diminution de la fréquence d'approvisionnement des jeunes otaries par leur mère au cours de la période d'élevage et de la réduction de leurs dépenses énergétiques. Aucun changement dans le nombre de plongées ou dans le temps passé à plonger par rapport au temps passé dans l'eau chaque jour n'a pu être détecté au cours de la période d'élevage des petits. La profondeur maximale moyenne de plongée augmente avec l'âge, mais diminue avec la masse des petits et la durée maximale des plongées est significativement plus longue en hiver qu'en été, indiquant un développement des aptitudes à la plongée des petits avec l'âge. L'effet positif de la taille du petit, indépendamment de son âge, sur les taux de plongée est le seul élément suggérant un effet des performances de croissance sur l'ontogenèse du comportement de plongée. L'absence de lien précis entre les performances de croissance, la masse et les performances de plongées des petits, mais aussi les grandes variations inter-individuelles du temps passé dans l'eau et des taux de plongées tendent à supporter l'hypothèse de l'existence de stratégies alternatives chez les petits d'*A. tropicalis* : consacrer plus de temps à la nage et à la plongée aux dépens de l'état de leurs réserves ou réduire leur niveau d'activité pour permettre d'augmenter l'état des réserves afin de maximiser leur taux de survie après le sevrage.

Introduction

Many mammal studies have shown that postweaning survivorship is related to weaning mass (Festa-Bianchet et al. 1997, 2000; Lindström 1999). In pinnipeds, the probability of survival in the first year increased with body mass and condi-

tion at weaning (Baker and Fowler 1992; McMahon et al. 2000; Hall et al. 2001). A significant positive relationship between pup growth rate and individual postweaning survival was also detected in subantarctic fur seals (*Arctocephalus tropicalis* (Gray, 1872)) (Beauplet et al. 2005a), and this effect was greater for males than for females. Interestingly, the

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pup growth rate was found to take precedence over pup weaning mass in its positive effect on postweaning survival (Beauplet et al. 2005a).

As reported in previous pinniped studies, heavier weaners exhibit greater diving capabilities (Kooyman 1989; Hindell et al. 1999) and reduced heat loss because of their higher blubber content (Bryden 1964) and larger size (Peters 1983). They are therefore expected to have an advantage over lighter pups by being able to spend more time searching for food during the first months of nutritional independence. We therefore hypothesize that successful weaning is likely to be associated with strong selection for the development of efficient swimming and diving capabilities prior to the weaning process.

In most otariids, particularly fur seals, offspring remain on the breeding island, since they are dependent upon maternal milk until they are weaned (Trillmich 1996); this allows precise assessment of the preweaning rate of growth in mass and length (Chambellant et al. 2003). Assessment of pup growth in most sea lion species can only be achieved during the first few months, as mother and pup can travel together to several haul-out locations until weaning (K. Ono, personal communication). Otariid seals (fur seals and sea lions) have a lactation pattern characterized by short (1–2 days) nursing periods ashore alternating with short to long (2–30 days) maternal foraging trips to sea (Gentry and Kooyman 1986; Francis et al. 1998; Georges and Guinet 2000; Bailleul et al. 2005). For most of the lactation period, fur seal pups are entirely dependent on the mother for nutritional input (Bonner 1984). The pups exploit maternal milk to grow in size and mass, but also accumulate fat stores (Beauplet et al. 2003), which represent an excellent insulator (Bryden 1964; Blix et al. 1979) and also provide essential nutrients to sustain them from weaning to complete nutritional independence (Bryden 1968; Hindell et al. 1994). Such an abrupt interruption of parental care is thus a crucial step in the life history of the animal (Oftedal et al. 1987; Bowen 1991), as newly weaned pups face a number of critical challenges, including escaping from predators and learning to locate and capture prey.

Throughout their lactation period, otariid pups are observed to spend time swimming and diving at sea (Horning and Trillmich 1997; McCafferty et al. 1998; Baker and Donohue 2000). An alternative hypothesis — though the two hypotheses are not mutually exclusive — to explain the enhanced survival rates in faster growing pups is that they can allocate more energy and consequently more time to developing their swimming and diving abilities than slower growing pups can. Consequently, they may exhibit more complete development of their preweaning foraging skills. The ontogeny of motor activities and physical fitness is assumed to have a significant influence on future foraging efficiency and breeding success in carnivores (for a review see Bekoff 1989). With respect to development, we expect that individuals in a better nutritional state would be able to allocate more time to training at sea than pups in poorer condition, and this should have a positive effect on their physical fitness and subsequent postweaning survivorship.

Among fur seal species, the time from birth to weaning ranges from 4 months to 3 years (Gentry and Kooyman 1986), with tropical and subtropical species having long lactation periods of 10 months to 3 years. Such species are pre-

sumed to have developed considerable swimming and foraging experience by the time they are weaned, as is found in Galápagos fur seal (*Arctocephalus galapagoensis* Heller, 1904) pups (Horning and Trillmich 1997). Among the two subpolar species, northern fur seals (*Callorhinus ursinus* (L., 1758)) appeared to have limited diving experience at weaning (Baker and Donohue 2000), while Antarctic fur seals (*Arctocephalus gazella* (Peters, 1875)) in South Georgia were found to develop precocious diving skills in such a way that they exhibited diving abilities at weaning that allowed them to exploit prey similar to those taken by adults (McCafferty et al. 1998). During the final stages of lactation, fur seal pups are believed to supplement their diet with solid food (Doidge et al. 1986; Trillmich 1996; McCafferty et al. 1998).

We documented the ontogeny of the swimming and diving behaviours of subantarctic fur seal pups over their 10 months of lactation and investigated the possible effect of growth performance, age, and changes in nutritional state and environmental conditions. Our working hypotheses were that pups that were faster growing and those in a better nutritional state would devote more energy and time to swimming and diving, and that such pups would exhibit better diving performance than slower growing pups.

Materials and methods

Study site and model

The study was carried out during the 2002–2003 breeding season at La Mare aux Eléphants breeding colony located on the northeast side of Amsterdam Island (37°55'S, 77°30'E) in the southern Indian Ocean. Amsterdam Island is up to 400 km from the subtropical front.

In subantarctic fur seals, births occur from late November to early January, with a mean parturition date in mid-December (Georges and Guinet 2000). The nursing period lasts about 10 months (Tollu 1974; Georges et al. 1999), after which newly weaned pups leave their native island to acquire nutritional independence (Chambellant et al. 2003). During the birthing season, subantarctic fur seal pups were sexed and identified at birth by gluing a unique numbered piece of plastic tape on the top of the head. At about 1 month of age, at a mass of approximately 8–10 kg, each marked pup was tagged in the connective tissue on the trailing edge of both foreflippers with an individually numbered plastic tag (Dalton Rototags, Dalton Supplies Ltd., Nettlebed, Henley-on-Thames, UK).

At-sea behaviour

During this study, MK7 and MK9 time–depth recorders (TDRs) (Wildlife Computers, Redmond, Washington, USA) were deployed on pups throughout the rearing period. Known-age pups were captured the day after the departure of their mother to sea (i.e., the beginning of the fasting period), and TDRs were glued using two-part Araldite® (AW 2101 / HW 2951, Vantico AG, Basel, Switzerland) on the short hair on the upper part of a pectoral flipper. This area was chosen to reduce the possible effect on heat regulation of gluing the TDR on the body fur. Seals were captured by hand and subsequently weighed (± 0.05 kg) using a digital suspension balance (25 kg capacity, Salter Brecknell,

ElectroSamson™, Fairmont, Minnesota) and a standard-length measurement was also recorded to the nearest centimetre with the animal in a straight belly-down position. During the TDR-deployment period, pups were weighed every 2–3 days to monitor changes in pup mass. Most TDRs were retrieved after a minimum of 5 full days, though some were left for the whole fasting period and retrieved when the mother had returned to shore or just after her next departure. Upon TDR retrieval, data were downloaded directly to a portable laptop computer and TDR records were converted from hexadecimal format to decimal format using Hexdecode software (Wildlife Computers). Both MK7 and MK9 TDRs were equipped with a salt-water switch, which indicated when the pup was in the water (wet) or on land (dry).

Offset and drift of the pressure transducers were corrected using a customised program developed by N. Servera and written in R language (Ihaka and Gentleman 1996). The depth resolution of the TDRs was ± 1 m. Pups were considered to be diving when the depth was below 2 m, which was two times the nominal accuracy of the TDRs (Arnould and Hindell 2001; Schreer et al. 2001; Lea et al. 2002).

All TDRs were programmed to record pressure every second when wet. Basic parameters, such as the time at the beginning and at the end of a water bout, allowed calculation of water-bout durations, daily amount of time spent in the water (TW), number of dives, dive duration (D_{duration}), and maximum dive depth (Max. D_{depth}); descent and ascent speeds during a dive were extracted from the decimal files using customised software (N. Servera). To describe individual diving behaviour we calculated the mean dive duration (Mean D_{duration}) and mean dive depth (Mean D_{depth}) over the whole deployment period. The percentage of time spent in the water during the day was also calculated for 12 periods of 2 h defined from midnight to midnight. We defined the dive rate (DR_n , dives·h⁻¹) as the mean daily number of dives divided by the mean TW. We also calculated the dive rate in time (DR_h , %) as the amount of time spent diving while the pups were in the water, using the following equation:

$$DR_h = \frac{\text{mean daily amount of time spent diving}}{\text{mean TW}} \times 100$$

Some dive artefacts only observed with the MK7 TDRs had to be removed. These artefacts, characterized by a rapid increase in pressure and followed by a period of gradual decrease in pressure to the nominal surface value, only occurred when the animal was entering the water and could be eliminated by filtering the data and excluding all dives with a descent speed higher than 4 m·s⁻¹ and (or) a duration longer than 300 s. Such dive artefacts can result from prolonged contact of the pressure sensor of the TDR with a rock when pups are resting in pools.

The diving behaviour of pups was recorded from February to August. Independently of pup age, TDRs were deployed over two clumped periods: summer (February–March), when the pup age was 68 ± 7 days (mean \pm SE) ($n = 11$; range 57–83 days) and winter (May–August), when the mean age was 190 ± 40 days ($n = 14$; range 123–252 days). The data were obtained over a broader period of time in the winter than in the summer, initially covering the fall (May–June) and winter (July–August) periods. However, as there were no differ-

ences in diving behaviour between fall and winter we pooled all the data for that period of time, which we termed winter (May–August). Calculation of local times of sunrise, solar noon, and sunset was based on the procedure provided by the US National Oceanic and Atmospheric Administration (<http://www.srrb.noaa.gov/highlights/sunrise/sunrise.html>).

Pup growth

In 2002–2003, 100 pups were identified at birth at Amsterdam Island and were weighed from birth to weaning, which allowed us to calculate individual growth rates (Chambellant et al. 2003). Pups were weighed once every 2 weeks and measured once a month through the whole pup-rearing period. We defined an initial growth rate in mass and length, which was calculated when the pups were between 0 and 60 days of age; a growth rate encompassing a longer period was calculated when the pups were between 0 and 220 days of age.

Pup body condition and mass change when fasting

A body condition index (BCI) of the pups was determined from the residual value of the linear regression of mass (kg) against standard length (cm). This parameter was found to be independent of the lengths of the mothers and pups ($P = 0.99$ in both cases), and was thus preferred to the usual ratio, mass (kg) / standard length (cm), as the latter parameter is not independent of pup length (see Guinet et al. 1998). To determine the relationship between mass and length of the pups over the study period, we randomly sampled one measurement each of mass and length per pup to respect the independence criterion. The best relationship between pup mass and length was found to be exponential ($\mu = 0.279e^{0.044X}$ ($r^2 = 0.88$, $n = 108$, $P < 0.001$)), and the data were therefore log-transformed. We then calculated the BCI of the pup as the difference between the observed mass and the expected mass of the pup (μ) according to its length, and used the above equation.

When the pups were fasting, we calculated the mass-specific rate of mass loss (%·day⁻¹) according to the following relationship:

$$(\ln(m_f) - \ln(m_i)) / \Delta t \times 100$$

where m_i is the initial mass of the pup when first equipped, m_f is the final mass of the pup when the equipment was retrieved, and Δt is time (days) elapsed between the two captures.

Environmental conditions

The data on air temperature, rainfall, and wind speed were obtained from the weather stations on the island. The temperature used in this study was that measured during the hottest period of the day (2 p.m. UHT), rainfall was the total number of millimetres falling in a day, and wind speed was the mean of the maximum wind speed measured at 10-min intervals.

Faecal analyses

To investigate whether pups were reaching nutritional independence before they were fully weaned, faecal samples were collected throughout the winter period during the 2001/2002 (35 scats) and 2002–2003 (30 scats) breeding

Table 1. Summary of TDR deployments and successful recordings on subantarctic fur seal (*Arctocephalus tropicalis*) pups at Amsterdam Island during the austral summer and winter of 2003.

	No. of pups equipped / no. of recordings analysed	No. of males equipped / no. of females equipped	No. of males' recordings analysed / no. of females' recordings analysed*
Summer	11/11	4/7	4/7
Winter	17/14	9/8	8/6
Total	28/25	13/15	12/13

*The numbers of TDR-equipped male and female pups that provided recordings that were subsequently analysed.

seasons from pups whose mother had been at sea for at least 15 days. Faecal samples were obtained by stimulating faecal excretion through the injection of 5 mL of a laxative agent (Microlax®, Pfizer, 75668 Paris CEDEX 14, France) into the large intestine from the anus. Pups were then kept in an enclosure until scat collection, which usually occurred 5–10 min after the injection. Individual scat samples were stored frozen (–20 °C) in individual plastic bags until laboratory analysis. Faecal samples were then elutriated overnight and subsequently thawed in warm water and rinsed through 1.0 and 0.5 mm mesh sieves to collect any hard prey remains for subsequent prey-species analysis.

Statistical analyses

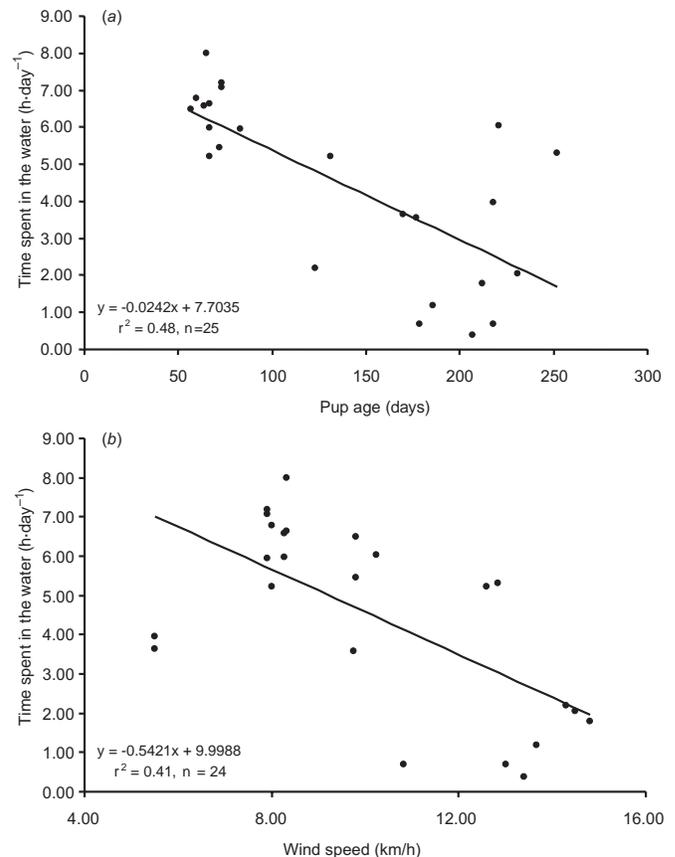
All statistical analyses were performed with SYSTAT® version 9.0 statistical software (SPSS Inc. 1999).

The amount of time spent in the water, number of dives, mean dive depth, and dive duration were analysed using ANOVA, with sex as a categorical factor, while age, body mass and condition, growth rate, mass-specific rate of mass loss of the pup, rainfall, and wind speed were used as covariates. When multivariate analyses were used, correlations were analysed using a general linear model (GLM), and the contribution of significant factors was assessed using backward stepwise analyses (level of rejection $P > 0.1$). Unless otherwise stated, values are reported as the mean \pm SE and statistical significance was considered to be $P < 0.05$.

Results

During this study, TDRs were deployed on 28 pups, of which 25 provided successful dive records (Table 1) for a total of 183 days of recording. The youngest pup equipped was 57 days of age while the oldest was 252 days of age at the beginning of the deployment period. In summer, 11 pups (4 males and 7 females) were equipped, for a total of 77 days (mean deployment period 7.0 ± 2.0 days), and in winter, 14 pups (6 females and 8 males) were equipped, for a total of 106 days (mean deployment period 7.6 ± 3.9 days).

The fasting and TDR deployment periods, and consequently the number of days of recording available per pup, varied among pups. However, within TDR-deployment sessions we found no variation in the amount of time spent in the water, number of dives, maximum dive depth, average dive depth, and average and maximum dive depths in relation to the fasting stage (in days). Based on this result, we calculated Mean TW, mean number of dives per day, Mean D_{duration} , and Mean D_{depth} over the whole TDR-deployment period for each of the pups in the study, while maximum dive depth and dive duration were extracted over the whole TDR-deployment period.

Fig. 1. Relationship between the mean daily time spent in the water and pup age (a) and wind speed (b).

The mean delayed growth rate of the 25 pups successfully equipped with TDRs was 61 ± 26 and 33 ± 14 g at 60 and 220 days, respectively.

TW values during fasting

Over the whole rearing period, pups spent 4.40 ± 2.39 h-day⁻¹ ($n = 25$) in the water. TW (h-day⁻¹) decreased in relation to pup age (days) ($t = -3.08$, $n = 25$, $P = 0.005$; Fig. 1a), and was negatively related to wind speed (m·s⁻¹) ($t = -2.60$, $n = 25$, $P = 0.016$; Fig. 1b) according to the following equation:

$$TW = -0.018 \text{ age} - 0.312 \text{ wind speed} + 10.058$$

$$(n = 25, r^2 = 0.60, P = 0.001)$$

No other factors were found to have a significant effect on TW. The highest TW values in a single day were 13.5 h in summer and 12.5 h in winter. In contrast to summer, winter

Fig. 2. Distribution of the percentages of time spent in the water among 2-h periods in summer (solid bars) and winter (open bars).

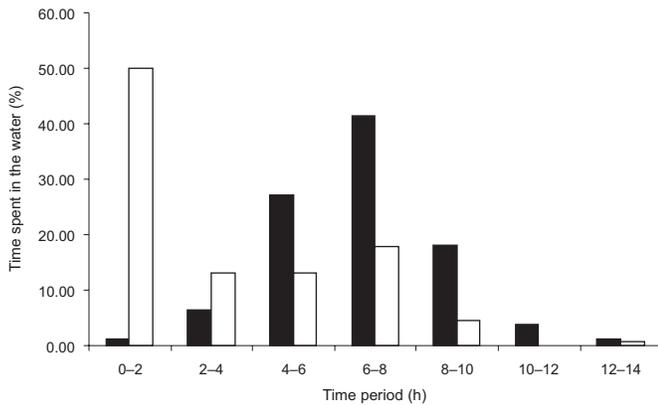
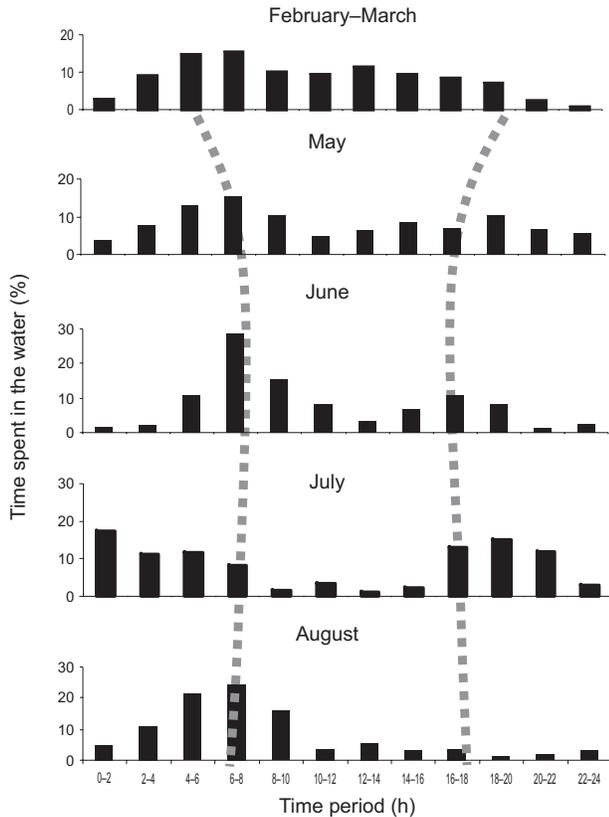


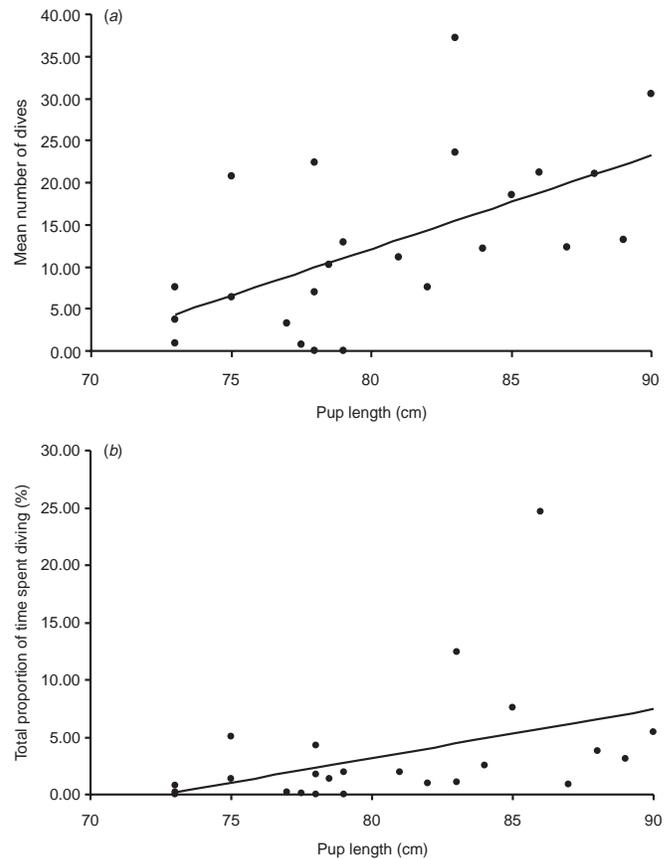
Fig. 3. Distribution of the percentages of time spent in the water among 2-h periods throughout the study period. The dotted line indicates the change in sunrise and sunset hours.



was characterized by a sharp increase in the number of days (50%) during which pups did not go into the water or remained at sea for less than 2 h (Fig. 2).

The temporal distribution of the pups' swimming activity throughout the day for each season on Amsterdam Island is shown in Fig 3. There is an apparent and gradual shift in the greatest amount of time spent in the water from mainly during daylight hours in summer, to dawn and dusk in fall, to mainly at night in winter.

Fig. 4. Changes in the mean daily dive rate, expressed as the number of dives (DR_n in the text) (a) and in the proportion of time spent diving (DR_h in the text) (b) while pups were in the water, according to pup length.



Diving activity

The TDR-equipped pups performed a total of 8803 dives to 3 m or deeper over the whole study period.

Dive rate

The mean daily number of dives was related to TW ($r^2 = 0.28$, $n = 25$, $P = 0.008$). One pup was an outlier (studentized residual = 11.0) and was thus removed from the analyses. No differences between summer and winter were found in DR_n (Kruskal–Wallis test, $n_1 = 10$, $n_2 = 14$, $U = 78$, $P = 0.64$) or DR_h (Kruskal–Wallis test, $n_1 = 10$, $n_2 = 14$, $U = 47$, $P = 0.17$). Mean DR_n was 12.7 ± 10.0 dives per hour spent in the water ($n = 24$) and DR_h was $3.4\% \pm 5.4\%$. Neither DR_n nor DR_h varied according to pup age or sex, but both were positively related to pup size according to the following equations:

$$DR_n = 1.11 \text{ size} - 76.70$$

$$(n = 24, r^2 = 0.33, P = 0.003; \text{Fig. 4a})$$

$$DR_h = 0.43 \text{ size} - 30.87$$

$$(n = 24, r^2 = 0.17, P = 0.047; \text{Fig. 4b})$$

Fig. 5. Distribution of maximum dive durations (Max. D_{duration} in the text) in summer (solid bars) and winter (open bars).

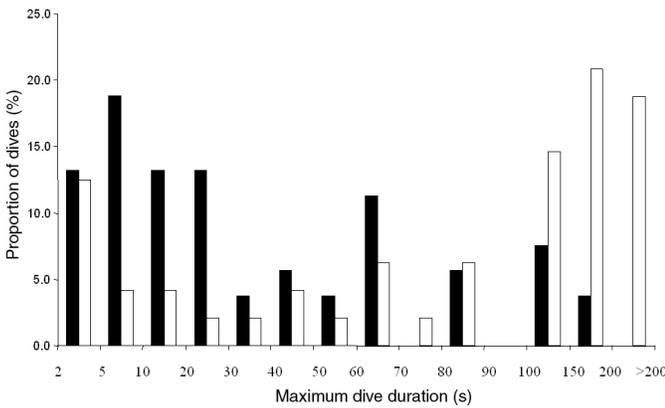


Fig. 6. Distribution of maximum dive depths (Max. D_{depth} in the text) in summer (solid bars) and winter (open bars).

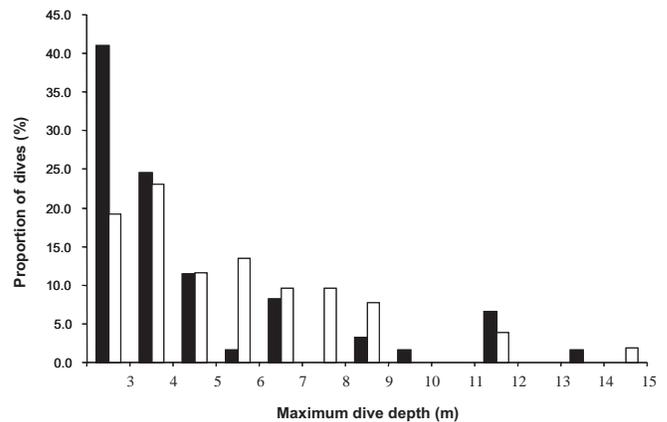


Table 2. Numbers of pup scats sampled during winter that contained prey remains.

	July	August	September	October	Total
No. of scats analysed	18	21	23	3	65
No. with fish remains only	0	0	0	0	0
No. with crustacean remains	0	0	1	0	1
No. with fish and crustacean remains	0	0	2	0	2

Dive duration

One pup was excluded from the analyses, as it performed no dives during the TDR-deployment period. Mean D_{duration} throughout the pup-rearing period was 8.3 ± 9.6 s ($n = 24$) and did not vary according to pup age ($P > 0.05$). However, Mean D_{duration} was found to vary according to pup sex ($F_{[1,23]} = 4.33$, $P = 0.05$) and pup BCI ($F_{[1,23]} = 4.24$, $P = 0.05$). When categorizing by sex, no relationship was found between BCI and Mean D_{duration} for female pups ($n = 13$, $P = 0.46$), while Mean D_{duration} was found to increase in relation to BCI for male pups (Mean $D_{\text{duration}} = 0.14\text{BCI} + 0.093$; $n = 11$, $r^2 = 0.44$, $P = 0.043$).

Max. D_{duration} was 109.8 ± 91.3 s ($n = 24$) and was found to increase with pup age ($t = 2.90$, $n = 24$, $P = 0.009$) and TW ($t = 3.23$, $n = 24$, $P = 0.004$) according to the following equation:

$$\text{Max. } D_{\text{duration}} = 0.91\text{age} + 29.82\text{TW} - 155.24$$

$$(n = 24, r^2 = 0.35, P = 0.011)$$

The percentages of dives according to maximum dive durations are shown in Fig. 5.

Dive depth

Modal D_{depth} was 3 m in summer and 4 m in winter (Fig. 6). Mean D_{depth} over the whole pup-rearing period was 3.4 ± 0.4 m ($n = 24$), and was found to increase with age (days) ($t = 2.64$, $n = 25$, $P = 0.015$) and decrease with pup mass (kg) ($t = -2.93$, $n = 25$, $P = 0.008$) according to the following equation:

$$\text{Mean } D_{\text{depth}} = 0.01\text{age} - 0.24\text{mass} - 1.69$$

$$(n = 24, r^2 = 0.30, P = 0.02)$$

However, no significant change in maximum dive depth could be detected throughout the study period.

Prey consumption

The 65 pup scats collected between July and October (Table 2) were searched for prey remains. The fasting period for the pups sampled was 26 ± 13 days (range 5–46 days).

Prey remains were found in three scats sampled in September from pups who had fasted for 13, 28, and 32 days. Two scats contained crustaceans with one fish otolith in one scat and one fish bone in the other, while one scat had only crustacean remains.

Discussion

The unexpected result of this study was a decrease in the amount of time pups spent in the water throughout the rearing period, from 23% in summer to only 11% in winter. This is the opposite to the result found in *A. gazella* (McCafferty et al. 1998) and *C. ursinus* (Baker and Donohue 2000), in which the amount of time spent by the pup in the water increased with pup age to reach approximately 35% prior to weaning. The difference in the ontogeny pattern between *A. tropicalis* pups at Amsterdam Island and *A. gazella* and *C. ursinus* pups could be related to the difference in the duration of the lactation period between these species. Both *A. gazella* and *C. ursinus* have to fully develop their diving aptitude over a 4-month period compared with 10 months for *A. tropicalis*. Consequently, the only option for the two short-lactation species could be to increase both the amount of time spent in the water and their diving performance through the lactation period compared with *A. tropicalis* pups. One way to address this question independently of the possible effect induced by the differences in environmental

conditions (water and air temperatures, local food availability, etc.) would be to investigate the ontogeny of the swimming and diving behaviours of *A. gazella* and *A. tropicalis* pups in locations where they are sympatric.

The decrease in the amount of time spent in the water by older *A. tropicalis* pups compared with younger ones could also be related to the reduction of the pups' energy expenditure in relation to the decreasing rate of delivery of nutrient by the mother during late fall and winter, when food availability is lower (Georges and Guinet 2000; Beauflet et al. 2003). Lactating subantarctic fur seals at Amsterdam Island exhibit one of the longest foraging trip duration (Georges and Guinet 2000; Beauflet et al. 2004), delayed sexual maturity, and early senescence (Beauflet et al. 2005b), suggesting that this fur seal population, over the last decade, was living in an environment of low food availability. In that regard, food availability during the study year (2002–2003) was similar to that observed over the period 1995–2003. The mean growth rate of the 25 pups successfully TDR-equipped in 2002–2003 was in the upper range of the pup growth rates monitored annually over the period 1995–2003 (Chambellant et al. 2003; unpublished data).

The decreasing growth rate between the pup ages of 60 and 220 days reflects the decrease in maternal provisioning rate between summer and winter when mothers are confronted with adverse environmental conditions. Indeed, in a previous study Guinet and Georges (2000) showed that daily mass gain of the pup consecutive to a foraging trip decreases from 300 g per day spent at sea by the mother in summer to less than 150 g in winter, when pups were 250 days old. The maximum rate of mass loss was reached when pups were about 120 days old. The decrease in mass-specific energy expenditure after 120 days of age could reflect better thermoregulation of *A. tropicalis* pups resulting from a change in body composition and properties of the fur when pups have completed their moult at about 4 month of age (Arnould et al. 2003; Beauflet et al. 2003). The insulation property of the fur, particularly in water, was found to improve after fur seal pups completed their moult (Arnould et al. 2003). It was also suspected that *A. tropicalis* pups on Amsterdam Island decreased their overall activity on land and at sea, and adopted an energy-saving strategy. Beauflet et al. (2003) reported a lower field metabolic rate in Amsterdam Island fur seal pups before and after the moult than in pups of any other fur seal species investigated to date. Their hypothesis appears to be confirmed by this study, which showed that pups were reducing the amount of time spent in the water with increasing age despite their better fur insulation. Furthermore, there was no evidence that despite shorter periods of time spent in the water in winter, pups were increasing their diving effort in terms of the number of dives performed or the total amount of time spent diving while in the water. Pup size is the only factor, independent of pup age, that suggests that faster growing pups were able to devote more time to diving. In contrast to this finding, both *A. gazella* and *C. ursinus* pups were found to increase the amount of time spent in the water after completion of the moult. Hence, we suspect that the decrease in the daily amount of time spent in the water by older *A. tropicalis* pups in our study was related to an energy-sparing strategy that was reflected by the observed decrease in the metabolic rate

(Beauflet et al. 2003). In winter, the water temperature ranges from 9 to 11 °C, and heat loss is likely to be higher in the water than on land, given the high thermal conductivity of water. Furthermore, when pups are in the water, they are generally more active; consequently, their energy expenditure is likely to be higher than on land, where they spent most of their time resting in sheltered locations (personal observations). This result seems to be further confirmed by the negative influence of wind speed on the amount of time pups were spending in the water, while sea state had no significant effect. On land, the cooling rate is likely to be higher on windy days, and pups may therefore reduce their overall energy expenditure by reducing the amount of time spent in the water during these windy periods. According to these results, we believe that the time pups can spend in the water is likely to be influenced by their thermoregulatory aptitude, as underlined by Baker and Donohue (2000), but other factors such as the energy-delivery rate also mediate the amount of time spent in the water. However, at the individual level, despite large interindividual variability in the amount of time spent in the water by older pups (Fig. 1), no explanatory variables were identified. In a previous study based on the large differences in interindividual field metabolic rate and mass-specific rate of mass loss (Beauflet et al. 2003), it was suggested that two different strategies were exhibited by the pups. One consisted of minimizing energy expenditure, either when pups' body reserves are too small to sustain a greater amount of activity or, in larger pups, by reducing their field metabolic rate to maximize their growth rate, and the other one consisted of allocating more energy to swimming and diving.

In summer, heat loss in the water may also not be a major issue for the pups born on Amsterdam Island, as water temperatures during that season generally ranged between 17 and 20 °C. Pups may also use the high thermal conductivity of water compared with air to facilitate thermal homeostasis because overheating on land could be the issue, as several pups have been found to succumb to heat shock, since the ground temperature reaches over 40 °C within the colony on a sunny day. Interestingly, during summer most of the at-sea activity took place during daylight hours, and mostly in seawater pools along the shore, with the highest frequency of swimming at sunrise. As pups aged, swimming activity shifted progressively to dawn and dusk hours, and during the winter months, prior to weaning, most swimming activity took place at night, with the greatest activity after sunset and before sunrise. The winter activity pattern of the pups tended to be similar than that of adult female *A. tropicalis* from Amsterdam Island, which dive exclusively at night (Georges et al. 2000). Similar trends were described for *A. gazella* (McCafferty et al. 1998), *A. galapagoensis* (Horning and Trillmich 1997), and *C. ursinus* (Baker and Donohue 2000), as pups of these species exhibited crepuscular peaks in swimming and diving activity when close to weaning, and these activity/foraging patterns were similar to those of adult females.

While the daily amount of time spent in the water was decreasing with age, pups were developing their diving abilities by performing deeper and longer dives as they aged; however, diving effort was found to increase with age, and only pup size but not pup age could explain the change in

pups' dive rates. The mean dive duration was found to be related to BCI in male pups but not in female pups, and this intersexual differences could possibly be explained by the sex differences in body composition between male and female pups: for a given BCI, male pups are leaner and more muscular than female pups (Beauplet et al. 2003), and consequently should dispose of greater oxygen stores than females. This is consistent with the observed sex difference in mean dive duration, although this point needs to be investigated further. The maximum dive depth performances remained modest compared with those observed in adult females, the deepest dive observed being only to 15 m and with no differences between summer and winter. Mean dive depth was found to increase with age but decrease with pup mass; however, these relationships remain unclear and need further investigation. They suggest that heavier pups, for a given age, were fatter and consequently more buoyant and less able to dive deep than were leaner pups.

The most striking change observed was the large increase in maximum dive duration, with some dive exceeding 200 s in winter time. This increase in diving performance, particularly maximum dive duration, is likely to be related to the development of physiological capability with pup age through the increase in blood and muscle oxygen stores as pups grow, and suggests that dive duration (i.e., the level of oxygen stores) rather than dive depth is a major contributing factor to the future diving performance of these pups. Consistently, haematocrit content was found to increase with pup age in both *A. gazella* and *A. tropicalis* pups (S. Luque, J.P.Y. Arnould, and C. Guinet, unpublished data), and with an increase in muscular oxygen stores, owing to larger muscle mass and myoglobin content (Burns and Castellini 1996).

The results of this study suggest that the diving performance of *A. tropicalis* pups prior to weaning was still limited in terms of mean and maximum dive depths and mean dive duration. There is no real evidence that pups were consuming a large amount of prey before weaning and the occurrence of prey remains seems to be anecdotal, with less than 5% of the scats containing few prey remains, which suggests that prey consumption represented a small contribution, if any, to the energy supply of the pups before weaning.

At this stage, we can only hypothesize that the strategy of *A. tropicalis* pups relies on a balance between swimming and diving activities (this study) and saving energy (Beauplet et al. 2003) to match the low maternal provisioning rate in winter. This could explain the lack of a relationship between the pups' growth performance, BCI, and any parameters indicative of the diving and swimming abilities of the pups. Such a strategy may enable pups to minimize their mass loss during winter and to be weaned with the largest possible adipose store, despite their low provisioning rate. The level of the pup's body stores at weaning may be more important than preweaning swimming and diving practice for the subsequent survival of the pups, as weaning mass is the main determinant of postweaning survival (Beauplet et al. 2004). Hence, the level of adipose stores would determine how long the pup would be able to explore the marine environment to locate a favourable foraging location, and this may be more important than the amount of diving practice to its chances of survival (Beauplet et al. 2005a). Leaving earlier, i.e.,

through the winter, when pup mass is higher, is probably not a viable alternative strategy because food resources are low, as indicated by the mothers' foraging performance. Furthermore, the pups' energy expenditure in the colder water would be much higher than if they remained mostly resting on land waiting for environmental conditions and prey availability to improve in early spring. In future studies we should (i) confirm the existence of two alternative strategies (more developed swimming and diving abilities versus greater body stores at weaning) and (ii) investigate the outcome of these strategies in terms of the pups' postweaning survival rate.

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References

- Arnould, J.P.Y., and Hindell, M.A. 2001. Dive behaviour, foraging locations, and maternal attendance patterns of Australian fur seals (*Arctocephalus pusillus doriferus*). *Can. J. Zool.* **79**: 35–38.
- Arnould, J.P.Y., Luque, S.P., Guinet, C., Costa, D.P., Kingston, J., and Shaffer, S.A. 2003. The comparative energetics and growth strategies of sympatric Antarctic and subantarctic fur seal pups at Îles Crozet. *J. Exp. Biol.* **206**: 4497–4506
- Bailleul, F., Luque, S., Dubroca, L., Arnould, J., and Guinet, C. 2005. Differences in foraging strategy and maternal behavior between two sympatric fur seal species at the Crozet Islands. *Mar. Ecol. Prog. Ser.* **293**: 273–282.
- Baker, J.D., and Donohue, M.J. 2000. Ontogeny of swimming and diving in northern fur seal (*Callorhinus ursinus*) pups. *Can. J. Zool.* **78**: 100–109.
- Baker, J.D., and Fowler, C.W. 1992. Pup weight and survival of northern fur seals *Callorhinus ursinus*. *J. Zool. (Lond.)*, **227**: 231–238.
- Beauplet, G., Guinet, C., and Arnould, J.P.Y. 2003. Body composition changes, metabolic fuel use, and energy expenditure during extended fasting in subantarctic fur seal (*Arctocephalus tropicalis*) pups at Amsterdam Island. *Physiol. Biochem. Zool.* **76**: 262–270.
- Beauplet, G., Dubroca, L., Guinet, C., Cherel, Y., Dabin, W., Gagne, C., and Hindell, M. 2004. Foraging ecology of subantarctic fur seals *Arctocephalus tropicalis* breeding on Amsterdam Island: seasonal changes in relation to maternal characteristics and pup growth. *Mar. Ecol. Prog. Ser.* **273**: 211–225.
- Beauplet, G., Barbraud, C., Chambellant M., and Guinet, C. 2005a. Interannual variation in the post-weaning survival of subantarctic fur seals: influence of pup sex, growth rate, and environmental conditions. *J. Anim. Ecol.* In press.
- Beauplet, G., Barbraud, C., Dabin, W., Küssener, C., and Guinet, C. 2005b. Age-specific survival and reproductive performances in female subantarctic fur seals: evidence of senescence and individual quality. *Oikos*. In press.

- Bekoff, M. 1989. Behavioral development of terrestrial carnivores. *In* Carnivore behavior, ecology, and evolution. *Edited by* J.L. Gittleman. Chapman and Hall, London. pp. 89–124.
- Blix, A.S., Grav, H.J., and Ronald, K. 1979. Some aspects of temperature regulation in newborn harp seal pups. *Am. J. Physiol.* **236**: 188–197.
- Bonner, W.N. 1984. Lactation strategies in pinnipeds: problems for a marine mammalian group. *Symp. Zool. Soc. Lond. No. 51*. pp. 253–272.
- Bowen, W.D. 1991. Behavioural ecology of pinniped neonates. *In* Behaviour of pinnipeds. *Edited by* D. Renouf. Chapman and Hall, Cambridge. pp. 66–127.
- Bryden, M.M. 1964. Insulating capacity of the subcutaneous fat of the southern elephant seal. *Nature (Lond.)*, **203**: 1299–1300.
- Bryden, M.M. 1968. Growth and function of the subcutaneous fat of the elephant seal. *Nature (Lond.)*, **220**: 597–599.
- Burns, J.M., and Castellini, M.A. 1996. Physiological and behavioural determinants of the aerobic dive limit in Weddell seal (*Leptonychotes weddelli*) pups. *J. Comp. Physiol. B*, **166**: 473–483.
- Chambellant, M., Beauflet, G., Guinet, C., and Georges, J.-Y. 2003. Long-term evaluation of pup growth and preweaning survival rates in subantarctic fur seals, *Arctocephalus tropicalis*, on Amsterdam Island. *Can. J. Zool.* **81**: 1222–1232.
- Doidge, D.W., McCann, T.S., and Croxall, J.P. 1986. Attendance behaviour of Antarctic fur seals. *In* Fur seals: maternal strategies on land and at sea. *Edited by* R.L. Gentry and G.L. Kooyman. Princeton University Press, Princeton, N.J. pp. 102–114.
- Festa-Bianchet, M., Jorgensen, J.T., Berubé, C.H., Portier, C., and Wishart, W.D. 1997. Body mass and survival of bighorn sheep. *Can. J. Zool.* **75**: 1372–1379.
- Festa-Bianchet, M., Jorgensen, J.T., and Reale, D. 2000. Early development, adult mass, and reproductive success in bighorn sheep. *Behav. Ecol.* **11**, 633–639.
- Francis, J., Boness, D., and Ochoa-Acuna, H. 1998. A protracted foraging and attendance cycle in female Juan Fernandez fur seals. *Mar. Mamm. Sci.* **14**: 552–574.
- Gentry, R.L., and Kooyman, G.L. (*Editors*). 1986. Fur seals: maternal strategies on land and at sea. Princeton University Press, Princeton, N.J.
- Georges, J.-Y., and Guinet, C. 2000. Maternal provisioning strategy and pup growth in subantarctic fur seals on Amsterdam Island. *Ecology*, **81**: 295–308.
- Georges, J.-Y., Sevot, X., and Guinet, C. 1999. Fostering in a subantarctic fur seal. *Mammalia*, **63**: 384–388.
- Georges, J.-Y., Bonadonna, F., and Guinet, C. 2000. Foraging habitat and diving activity of lactating subantarctic fur seals in relation to sea surface temperature at Amsterdam Island. *Mar. Ecol. Progr. Ser.* **196**: 291–304.
- Guinet, C., and Georges, J.-Y. 2000. Growth in pups of the subantarctic fur seal (*Arctocephalus tropicalis*) on Amsterdam Island. *J. Zool. (Lond.)*, **251**: 289–296.
- Guinet, C., Roux, J.P., Bonnet, M., and Mison, V. 1998. Effect of body size, body mass, and body condition on reproduction of female South African fur seals (*Arctocephalus pusillus*) in Namibia. *Can. J. Zool.* **76**: 1418–1424.
- Hall, A.J., McConnell, B.J., and Barker, R.J. 2001. Factors affecting first-year survival in grey seals and their implications for life history strategy. *J. Anim. Ecol.* **70**: 138–149.
- Hindell, M.A., Bryden, M.M., and Burton, H.R. 1994. Early growth and milk composition in southern elephant seal (*Mirounga leonina*). *Aust. J. Zool.* **42**: 723–732.
- Hindell, M.A., McConnell, B.J., Fedak, M.A., Slip, D.J., Burton, H.R., Reijnders, P.J.H., and McMahon, C.R. 1999. Environmental and physiological determinants of successful foraging by naive southern elephant seal pups during their first trip to sea. *Can. J. Zool.* **77**: 1807–1821.
- Horning, M., and Trillmich, F. 1997. Ontogeny of diving behaviour in the Galapagos fur seal. *Behaviour*, **134**: 1211–1257.
- Ihaka, R., and Gentleman, R. 1996. R language for data analysis and graphics. *J. Comput. Graph. Stat.* **5**: 299–314.
- Kooyman, G.L. 1989. *Diverse divers*. Springer-Verlag, Berlin and Heidelberg.
- Lea, M.-A., Hindell, M., Guinet, C., and Goldsworthy, S. 2002. A multivariate approach to the classification of dive behaviour in Antarctic fur seals, *Arctocephalus gazella*. *Polar Biol.* **25**: 269–279.
- Lindström, J. 1999. Early development and fitness in birds and mammals. *Trends Ecol. Evol.* **14**: 343–348.
- McCafferty, D.J., Boyd I.L., and Taylor, R.I. 1998. Diving behaviour of Antarctic fur seal (*Arctocephalus gazella*) pups. *Can. J. Zool.* **76**: 513–520.
- McMahon, C.R., Burton, H.R., and Bester, M.N. 2000. Weaning mass and the future survival of juvenile southern elephant seals (*Mirounga leonina*) at Macquarie Island. *Antarct. Sci.* **12**: 149–153.
- Oftedal, O.T., Boness, D.J., and Tedman, R.A. 1987. The behavior, physiology, and anatomy of lactation in the Pinnipedia. *Curr. Mammal.* **1**: 175–245.
- Peters, R.H. 1983. *The ecological implications of body size*. Cambridge University Press, Cambridge.
- Schreer, J.F., Kovacs, K.M., and O'Hara Hines, R.J. 2001. Comparative diving patterns of pinnipeds and seabirds. *Ecol. Monogr.* **71**: 137–162.
- SPSS Inc. 1999. SYSTAT®. Version 9.0 [computer program]. SPSS Inc., Chicago.
- Tollu, B. 1974. L'otarie de l'île d'Amsterdam *Arctocephalus tropicalis* (Gray 1872). Ph.D. thesis, Université de Paris 7, Paris.
- Trillmich, F. 1996. Parental investment in pinnipeds. *Adv. Study Behav.* **25**: 533–577.