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In polytocous mammals, weakling neonates, but not their stronger littermates, benefit from specialized foraging

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Abstract

Adjusting foraging strategies is a common phenomenon within groups of animals competing for the same resource. In polytocous mammals, neonates concurrently compete for limited milk and alternate between two foraging (suckling) strategies: adaptable exploratory foraging with random sampling of teats, and ordered foraging with a tendency towards exploiting a particular suckling position. Some theoretical (game theory) models have shown that weaker siblings in particular benefit from foraging specialization (suckling order). Neonate piglets establish a well-defined suckling order that develops gradually and fluctuates throughout the lactation period, implying the existence of inter-individual differences in foraging strategies. We therefore analyzed suckling behavior in pigs to determine whether one foraging strategy was more beneficial to neonates in terms of their body weight and foraging environment. We found that intermediate and heavy littermates tended to adjust their suckling strategy according to the foraging environment; however, the selected foraging strategy did not affect their overall growth performance. Lighter individuals that consumed significantly less milk did not greatly alternate their foraging strategy according to the foraging environment, but their growth rate was significantly higher whenever they performed less-exploratory foraging behavior. Although suckling order appeared to be a relatively stable behavioral phenotype, it was beneficial exclusively for weaklings. These results confirm theoretical predictions and indicate that specializing in a suckling position is a beneficial strategy for weaker, light neonates. These findings suggest that physically weaker neonates might have driven the evolution of neonatal foraging specialization.

Key words: neonatal foraging strategy, pig, polytocous mammals, suckling

Heterogeneity in foraging behaviors/strategies is normally driven by intragroup competition for limited resources, whereby competing individuals strive to establish a foraging strategy with lower costs and higher benefits, leading to the evolution of foraging generalists or specialists (e.g., Schoener 1971; Schoener 1974). In social animals, for instance, individuals forage in close proximity, and coexisting individuals reduce local competition through resource (niche) partitioning while the overall niche size remains the same; this suggests that foraging specialization may reduce within-group conflicts,

making the ability to specialize a prerequisite for group living (Sheppard et al. 2018). However, the level of specialization can vary among the individual group members that benefit from variable foraging behavior (Bolnick et al. 2003; Svanbäck and Bolnick 2005; Robertson et al. 2015; Cloyed and Eason 2017; Sheppard et al. 2018).

Foraging strategies in social groups have been studied mainly in adult animals, and reports on the foraging strategies of neonate polytocous animals are scarce. Neonate polytocous mammals form

social groups (litters) in which they concurrently compete for access to the teats (maternal milk), and alternate between two foraging (i.e., suckling) strategies: random sampling of teats (foraging generalization), and a preference for a particular suckling position (foraging specialization). Neonates of many polytocous mammals exhibit at least a partial suckling order, namely, teat fidelity and/or udder preference (Skok 2018). However, such foraging specialization is not considered rigid. As seen in the pig (Skok and Gerken 2016), it is a gradually developing and fluctuating behavioral phenotype, implying that inter-individual differences in foraging strategies also exist.

The pig is a particularly interesting subject in terms of understanding the evolution of mother–offspring resource allocation (Drake et al. 2008). The domestic pig in particular can represent a valuable model system to study sibling competition and neonatal foraging strategies in polytocous mammals because of its highly variable neonatal competition load (ratio of litter size: number of teats, and neonatal body weight variability).

Our main hypothesis for this research was that neonatal foraging specialization (i.e., suckling order) in polytocous mammals is inherent to the weakest (inferior) siblings (proposed by Skok 2018). Using simplified theoretical (game theory) models, Skok (2018) proposed that weaker siblings in particular benefit from foraging specialization. We therefore analyzed piglet suckling behavior to determine whether any particular foraging strategy was more beneficial to neonates in terms of growth performance, based on their body weight and foraging environment characteristics/litter competition load (teat availability [TA], intra-litter body weight asymmetry), as well as milk yield. Using this explanatory approach, we investigated whether only weaker individuals benefited from being foraging specialists.

Materials and Methods

Animals
This study summarizes detailed data acquired from a series of direct observations on suckling behavior and body weight in domestic piglets. A total of 292 piglets from 34 litters of different breed types (commercial pig breeds and the Göttingen minipig breed) were included in the analyses. Observations of Göttingen minipigs were carried out at the Göttingen Minipig breeding station (Georg-August University Göttingen, Department of Animal Sciences, Germany), whereas observations of commercial breeds were carried out at the Pig Research Centre (University of Maribor, Faculty of Agriculture and Life Sciences, Slovenia).

Analysis 1
A total of 214 piglets from 26 litters were used for the analysis of suckling strategy. To cover a wide range of intra-litter competition, two pig breed types were included in the analyses. A more competitive suckling environment was represented by using commercial pig breeds (158 piglets from 14 litters) which normally have a relatively low number of teats available per piglet (in this study, the number of functional teats available per piglet ranged from 0.93 to 1.88); a less competitive suckling environment was represented by using Göttingen minipigs (56 piglets from 12 litters), with 1.63–7.00 functional teats available per piglet in this study. Importantly, the basic characteristics and dynamics of suckling behavior and the establishment of suckling order in minipigs do not differ from those of commercial pig breeds despite a generally less competitive suckling

environment, that is, when litters are large, suckling behavior resembles that of commercial breeds (see Skok and Gerken 2016).

Analysis 2
This analysis aimed to measure the milk consumption of the piglets, for which a total of 78 commercial piglets from eight litters were used.

Measurements and behavioral observations
For both analyses, the piglets were individually marked with different combinations of lines painted on their backs within 24 h postpartum and maintained throughout the experiment. The first direct observation was made within 24 h after birth.

Observations for Analysis 1 were then repeated in the middle and at the end of the first week of lactation (a total of three observations in week 1), when suckling behavior is most dynamic. Later, when suckling order (tendency to suckle at the same position) was largely established, observations were undertaken as follows: two observations in the second week of lactation (one at the beginning and one at the end of a given period), and an additional four observations evenly distributed throughout the third and fourth weeks of lactation. Each observation lasted for 3 h or until at least two consecutive successful sucklings had been recorded. The piglets were individually weighed on each day of observation.

Observations for Analysis 2 were repeated at the end of the first week, followed by three observations evenly distributed until the end of the third week of lactation; the last observation was performed on the final day of the lactation period. Two consecutive sucklings were recorded in each observation. Since the aim of this analysis was to measure the milk consumption of the piglets, which was estimated using the weigh-suckle-weigh technique, the piglets were prevented from having free access to the sow. When the sow started grunting and the piglets started begging for milk, all the piglets were weighed individually. When all the piglets had been weighed, they were then released to the sow. When post-massage started (i.e., teat stimulation after suckling/milk intake), the piglets were weighed again. The difference between the two readings was taken to represent the milk intake of the piglets. All the piglets with a negative weight difference or with <5 g of milk intake per suckling were considered to have urinated and/or defecated after suckling and were excluded from that set of measurements. The whole weighing procedure was completed within 5 min.

Parameters
The basic data included teat(s) that piglets sampled, that is, strove to occupy during nursing; and teat(s) which piglets actually suckled, that is, teat(s) occupied during milk let-down, which is characterized by specific grunting by the sow and motionless intensive suckling that normally lasts for approximately 10–20 s.

Suckling behaviors were evaluated separately within different periods of lactation, namely, week 1 (early lactation) and the rest of the lactation period (late lactation). Foraging (suckling) strategies were quantified using the following parameters:

a. Foraging investment is the average number of teats a piglet strove to occupy during a single nursing episode in a given period of lactation.
b. Foraging diversity of a piglet in a given period of lactation was calculated using Shannon's entropy:

$$Foraging\ diversity = -\sum_{i=1}^{N} p_i \ln p_i$$

where p_i is the proportion of nursing events in which the i-th teat was occupied or suckled by a given piglet. Shannon's entropy quantifies the uncertainty of predicting the identity of a teat in which a piglet was interested (the lower the value, the more strictly oriented the piglet was, with a value of 0 indicating that a piglet put all its effort/investment into a single teat).

Foraging output was determined using the following parameters:

a. Foraging payoff is the average number of teats that a piglet actually suckled in a single nursing episode during a given period of lactation.
b. Foraging cost is the average number of teats that piglets unsuccessfully invested in (strove to occupy but not suckle) in a single nursing episode during a given period of lactation (difference between foraging investment and payoff).
c. Growth rate, where the relative daily weight gain (rDWG) was calculated according to the initial body weight of each piglet:

$$rDWG = \frac{BW_j - BW_i}{(t_j - t_i) \times BW_i}$$

where BW_i and t_i are initial BW and age, respectively, for the given lactation period; and BW_j and t_j are BW and age, respectively, at the end of a given lactation period.

The foraging (suckling) environment was determined by two parameters: TA and within-litter body weight variability/asymmetry (BWcv). TA is an indicator of group/foraging density and was defined as the number of teats available per littermate, which depends on the number of teats and litter size. Within-litter body weight variability is an indicator of littermate body weight homogeneity/asymmetry and was evaluated using the coefficient of variation for any given lactation period.

Classes of piglet body weight

Piglets were divided into three classes of body weight, where the relative measure of body weight (rBW) was calculated as the proportion of the body weight of a piglet vs. the average body weight of the litter. A value <1 indicates below-average body weight, 1 indicates average body weight, >1 indicates above-average body weight. This value was calculated for each period of lactation.

Statistical analyses

Statistical analysis was carried out in the SAS statistical package (SAS Inc., Cary, NC, USA). For Analysis 1, the evaluations were performed separately for early (first week) and late lactation (the rest of lactation). For Analysis 2, the evaluations were performed for the whole lactation period. For subsequent analysis, continuous variables describing the suckling environment and strategies (relative body weight, TA, within-litter body weight variability, investment, and diversity) were transformed into class variables (rBW, TA, BWcv, investment class, and diversity class, respectively) using the 33rd and 67th percentiles as class limits, resulting in three class variables (low, medium, and high).

For Analysis 1, the effect of neonatal competition load (properties of the suckling environment) on suckling strategy (investment and diversity) and outputs (cost, payoff, and rDWG) was first evaluated using a general linear model (GLM) procedure with fixed effects of TA and BWcv separately for the different rBW classes.

Then, the benefits of different suckling strategies for pigs of different rBW were analyzed. The effect of rBW on diversity and investment (GLM procedure, a model with fixed effects of rBW) was tested first. In the next step, a more detailed analysis was performed to test the effect of suckling strategy (investment class and diversity class) on suckling outputs (payoff, cost, and rDWG) based on the rBW. Here, a GLM procedure with fixed effects of investment class, rBW, and their interaction (or diversity class, rBW, and their interaction) was used. All the results are presented as least squares (LS) means and their respective standard errors. Where the tested effects were significant ($P < 0.05$), differences between the groups were tested using Tukey's test. For Analysis 2, the effect of suckling strategy (investment class and diversity class) on suckling outputs (payoff, cost, and rDWG) and milk intake were evaluated based on the rBW. A GLM procedure with fixed effects of investment class, rBW, and their interaction (or diversity class, rBW, and their interaction) was used. The results are presented as LS means and their respective standard errors. Where the tested effects were significant ($P < 0.05$), differences between the groups were tested using Tukey's test.

Ethical approval

All applicable international, national, and/or institutional guidelines for the care and use of animals were followed, including ABS/ASAB guidelines for ethical analysis of animals.

Results

Analysis 1

Early lactation (Week 1)

The results showed that TA, but not within-litter body weight variability (BWcv), was a suckling environment feature that affected foraging strategy in the first week of lactation (Table 1).

In the case of TA, the heaviest piglets (rBW >1.07) appeared to be more prone to altered suckling strategies in accordance with the level of foraging competition. They showed not only a significantly higher foraging investment (1.66), but also higher foraging costs (0.52) in the low-density group (high TA, >1.56 teats available per littermate); foraging payoffs did not differ according to TA. Additionally, heavy siblings had significantly higher growth rates at both extremes of TA (0.153 when TA <1.23, and 0.152 when TA >1.56), that also appeared to be the case for medium body weight individuals; however, medium siblings did not show alterations in suckling strategy.

In light piglets (rBW <0.95), foraging costs appeared to be related to the TA, where weaklings suffered the highest foraging costs when the number of teats available per littermate was high (>1.56 teats per littermate; foraging costs of 0.52).

The results obtained on the benefits for piglets of different body weights of choosing different suckling strategies revealed that light siblings (rBW <0.95) had a higher growth rate when they exhibited less exploratory foraging behavior (Figure 2), this is, when they strove to suckle a low number of different teats within a single suckling event (foraging investment <1.2), as well as when the foraging diversity was low (<1). In siblings of medium and high body weights, the growth rate was not significantly different with respect to the foraging strategy.

Overall (all rBW classes), foraging payoff was affected by foraging investment: as the number of teats explored (foraging investment) increased, the number of teats suckled (foraging payoff) also increased, whereas the foraging cost increased significantly with

Table 1. Effect of suckling environment features (TA and BWcv) on foraging strategies and outputs in early lactation

	TA			BWcv		
	low (<1.23)	medium (1.23–1.56)	high (>1.56)	low (<0.14)	medium (0.14–0.17)	high (>0.17)
Light piglets						
Foraging investment	1.39 ± 0.08	1.28 ± 0.07	1.50 ± 0.07	1.41 ± 0.08	1.42 ± 0.06	1.34 ± 0.08
Foraging diversity	1.48 ± 0.18	1.29 ± 0.17	1.20 ± 0.16	1.07 ± 0.19	1.52 ± 0.15	1.39 ± 0.17
Foraging payoff	0.98 ± 0.04	1.00 ± 0.03	0.98 ± 0.03	1.06 ± 0.04	0.94 ± 0.03	0.96 ± 0.04
Foraging cost	0.40[ab] ± 0.07	0.28[a] ± 0.07	0.52[b] ± 0.06	0.35 ± 0.08	0.48 ± 0.06	0.37 ± 0.07
rDWG	0.113 ± 0.016	0.089 ± 0.015	0.112 ± 0.014	0.111 ± 0.017	0.112 ± 0.013	0.091 ± 0.015
Medium piglets						
Foraging investment	1.40 ± 0.11	1.30 ± 0.07	1.55 ± 0.08	1.47 ± 0.08	1.39 ± 0.09	1.40 ± 0.10
Foraging diversity	1.55 ± 0.20	1.32 ± 0.14	1.24 ± 0.15	1.41 ± 0.14	1.33 ± 0.16	1.39 ± 0.19
Foraging payoff	0.95 ± 0.05	1.03 ± 0.04	1.11 ± 0.05	1.01 ± 0.04	1.00 ± 0.04	1.08 ± 0.05
Foraging cost	0.45 ± 0.09	0.26 ± 0.06	0.45 ± 0.07	0.46 ± 0.06	0.39 ± 0.07	0.32 ± 0.09
rDWG	0.147[b] ± 0.012	0.109[a] ± 0.009	0.131[ab] ± 0.01	0.127 ± 0.009	0.136 ± 0.010	0.124 ± 0.012
Heavy piglets						
Foraging investment	1.39[a] ± 0.06	1.31[a] ± 0.07	1.66[b] ± 0.09	1.53 ± 0.08	1.41 ± 0.07	1.41 ± 0.07
Foraging diversity	1.50 ± 0.12	1.38 ± 0.13	1.05 ± 0.17	1.34 ± 0.16	1.30 ± 0.13	1.30 ± 0.13
Foraging payoff	1.03 ± 0.03	1.07 ± 0.03	1.13 ± 0.04	1.13 ± 0.04	1.06 ± 0.03	1.04 ± 0.03
Foraging cost	0.36[ab] ± 0.05	0.24[a] ± 0.05	0.52[b] ± 0.07	0.39 ± 0.07	0.36 ± 0.05	0.37 ± 0.05
rDWG	0.153[b] ± 0.010	0.111[a] ± 0.010	0.152[b] ± 0.014	0.129 ± 0.013	0.144 ± 0.010	0.143 ± 0.010

rBW, relative body weight (low <0.95, medium 0.95–1.07, high >1.07); rDWG, relative daily weight gain; BWcv, within-litter body weight variability.
[a,b] Different letters indicate significantly ($P < 0.05$) different least square means for TA and BWcv.

higher investment and diversity. Interestingly, a negative effect of foraging cost on growth rate was found only in light piglets (Figure 1).

Late lactation (after the first week)
After the first week of lactation, when the suckling dynamic on the udder was ceasing, the foraging strategy used by littermates of different body weights appeared to be more dependent on the foraging environment (Table 2). The effects of both TA and BWcv were most prominent in piglets of medium body weight (rBW 0.95–1.08), where all the foraging parameters were affected. Considerably higher foraging investment/diversity/payoff/costs were observed for less competitive foraging environment with more teats available per individual (>1.67), with no effect on growth rate. Similarly, values for all the traits (except foraging payoff) increased with higher BWcv (Table 2).

A comparable pattern was found in heavy individuals (rBW >1.08), with the highest foraging investment/payoff/costs observed in the foraging environment with a high number of teats available per littermate (>1.67), and increased foraging investment/cost observed with increased BWcv. However, none of the foraging environmental factors had a significant effect on foraging diversity or growth rate.

Similar to early lactation, foraging strategy was least affected by the foraging environment in light individuals (rBW <0.95). However, foraging investment and foraging payoff increased with increasing number of teats available, whereas BWcv affected only diversity and growth rate which were higher in litters with increased body weight asymmetry (Table 2). The latter was the case for all classes of body weight.

The benefits for piglets of different body weights of choosing different suckling strategies were in accordance with the results obtained for early lactation, and revealed that when light siblings exhibited less exploratory foraging behavior (low foraging investment), they obtained significantly higher benefits in terms of growth rate compared with their medium and heavy littermates (0.096 vs. 0.058 and 0.063, respectively). Contrary to the early lactation results, no differences were found in foraging diversity.

Regardless of the class of body weight, foraging cost and foraging payoff increased significantly with increasing foraging investment and increasing foraging diversity; however, the latter was not the case for light individuals (Figure 2).

Analysis 2
Milk intake
Suckling data were analyzed for the whole lactation period. Overall, the results for foraging payoff, foraging cost, and growth rate confirmed those obtained in Analysis 1 (Figure 3); notably, however, the results of Analyses 1 and 2 are not completely comparable because of the different methodologies used. The most important result of Analysis 2 was related to milk intake, which was not significantly affected by either foraging investment or foraging diversity (Figure 3) in any of the classes of body weight. However, milk intake appeared to be strongly dependent on body weight, with heavier individuals (rBW >1.13) presenting significantly higher milk consumption.

Discussion
Although conspecific individuals are normally considered ecological equivalents (i.e., they occupy a similar ecological niche in a similar environment), their level of specialization can vary depending on a variety of factors. These include body size/weight and ontogeny (Bolnick et al. 2003; Svanbäck and Bolnick 2005; Cloyed and Eason 2017), as well as the size and density of the social group, whereby the larger the social group is, the more specialized the foraging niches of individual group members are (Sheppard et al. 2018). Accordingly, in the present study, differences in foraging (suckling) strategies were found when the properties of a given social environment and body weight were included in the model. Compared with
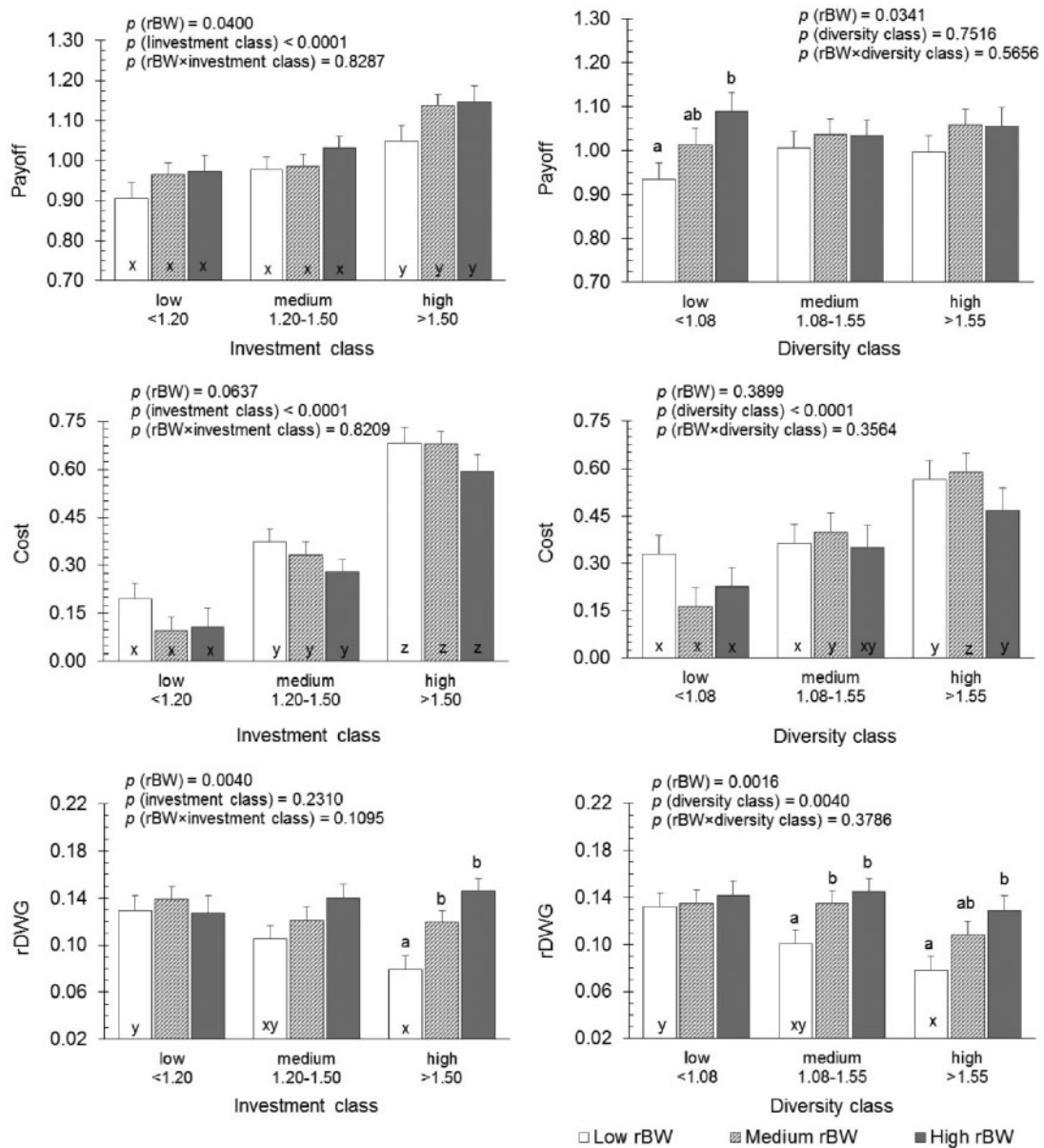
Figure 1. Effect of different suckling strategies on foraging payoff, foraging cost and growth rate in early lactation.
rBW, relative body weight (low <0.95, medium 0.95–1.07, high >1.07).
[abc]Different letters indicate significantly ($P < 0.05$) different least square means for rBW classes within each foraging investment (or diversity) class.
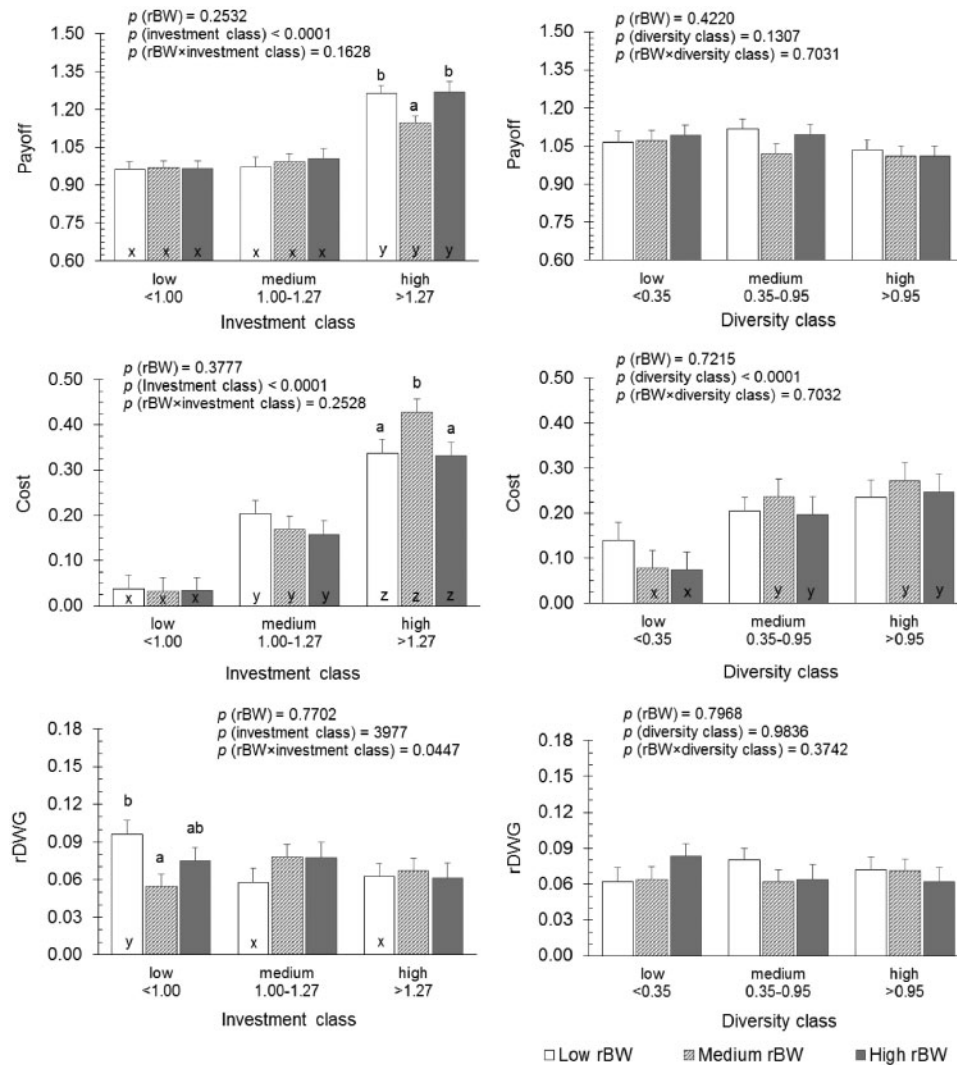[xyz]Different letters indicate significantly ($P < 0.05$) different least square means for foraging investment (or diversity) class within each rBW class.

piglets of low body weight, intermediate and heavy littermates showed a stronger tendency toward adjusting their suckling strategy in accordance with the characteristics of the litter/group they belonged to. Stronger siblings were more specialized at suckling positioning when their environment was characterized by low TA (i.e., high density at the udder) and lower within-litter body weight asymmetry. However, whichever foraging strategy littermates of medium or high body weight chose, their growth rate was generally not affected.

In contrast, littermates with low body weight did not alter their foraging strategy according to the foraging environment, except to some extent during late lactation. Yet piglets of low body weight, which consumed significantly less milk than their heavier littermates, could compensate in growth by choosing less exploratory,

more ordered foraging behavior; in this case, their growth performance improved significantly, likely because of the reduction in energy expenditure during suckling (foraging costs).

In the pig, a species with a well-defined suckling order, two different neonatal foraging strategies associated with lactation ontogeny are generally recognized. Piglets ultimately achieve a relatively stable specialization in exploiting a certain udder position (suckling order), but behave as foraging generalists without a specific orientation toward a suckling position at the beginning of lactation when they compete for colostrum (Skok and Škorjanc 2014). Increasing early competition (including aggression) within the group is thus reduced through mitigation of foraging overlap, also termed resource (niche) partitioning in animal ecology, which by definition leads to the evolution of foraging specialists (Schoener 1974).

Figure 2. Effect of different suckling strategies on foraging payoff, foraging cost and growth rate in late lactation.

rBW, relative body weight (low <0.95, medium 0.95–1.08, high >1.08).

[abc]Different letters indicate significantly ($P < 0.05$) different least square means for rBW classes within each foraging investment (or diversity) class.

[xyz]Different letters indicate significantly ($P < 0.05$) different least square means for foraging investment (or diversity) class within each rBW class.

In an intraspecific social group like a group of suckling piglets, individuals forage in close proximity and inevitably confront other group members, and thus individual strength and dominance value may have the most pronounced effect on the foraging dynamics and strategy within a certain environment (Gall and Manser 2018). Body size and weight generally represent a reasonable predictor of an individual's dominance value (Drickamer et al. 1973; Wauters and Dhondt 1989; Puppe and Tuchscherer 1999; Morgan et al. 2000) and foraging strategies (Weise et al. 2010; Orben et al. 2015; Price and Hopkins 2015), including home range size (Harestad and Bunnel 1979; Swihart et al. 1988; Tucker et al. 2014). In this context, larger individuals are generally accepted to be under reduced selection pressure because they can dominate resource use (Brown and Maurer 1986), which was the case in the present study. Littermates with body weight below the litter average received significantly lower amounts of milk compared with their heavier littermates—a known phenomenon in mammals (e.g., King et al. 1997; Wamberg and Tauson 1998; Riek 2008; Rödel et al. 2008; Hofer et al. 2016), which can be explained by the vigorousness of

mammary gland stimulation in the pig (King et al. 1997). According to Hofer et al. (2016), stronger mammalian littermates also skew milk intake in their favor through aggressive acts that cause subordinates to lose substantially more nursing time than dominants; hence, the difference in milk intake increases with increasing aggression during nursing. However, in this study, weaker littermates likely compensated for milk deficits with relatively more specialized foraging strategies (i.e., oriented to fewer, or even only one, suckling position), which increased their relative growth performance. By striving to persist with a particular position, the lightest (and likely inferior) individuals avoid excessive confrontations with their heavier and stronger littermates, thereby avoiding expenditure of extra energy on teat disputes in which they will most likely be outcompeted. The outcomes of teat disputes have been reported as being strongly related to piglet growth rate, especially in the early phase of lactation where the greatest number of wins relates to better growth (De Passillé et al. 1988). Therefore, greater foraging specialization decreases the number of unsuccessful attempts to obtain a suckling position (foraging cost), as was the case for all the classes of body

Table 2. Effect of suckling environment features (TA and BWcv) on foraging strategies and outputs in late lactation

	TA			BWcv		
	low (<1.20)	medium (1.20–1.67)	high (>1.67)	low (<0.14)	medium (0.14–0.21)	high (>0.21)
Light piglets						
Foraging investment	1.10[a] ± 0.06	1.26[a] ± 0.05	1.50[b] ± 0.06	1.20 ± 0.06	1.28 ± 0.05	1.38 ± 0.06
Foraging diversity	0.67 ± 0.09	0.61 ± 0.08	0.84 ± 0.09	0.47[a] ± 0.09	0.87[b] ± 0.08	0.78[ab] ± 0.09
Foraging payoff	0.92[a] ± 0.04	1.10[b] ± 0.04	1.24[c] ± 0.05	1.09 ± 0.04	1.05 ± 0.04	1.13 ± 0.04
Foraging cost	0.18 ± 0.04	0.16 ± 0.04	0.26 ± 0.05	0.12 ± 0.04	0.23 ± 0.04	0.25 ± 0.04
rDWG	0.093 ± 0.012	0.057 ± 0.010	0.072 ± 0.012	0.058[a] ± 0.011	0.066[ab] ± 0.01	0.098[b] ± 0.011
Medium piglets						
Foraging investment	1.13[a] ± 0.05	1.15[a] ± 0.05	1.49[b] ± 0.05	1.15[a] ± 0.04	1.25[ab] ± 0.05	1.37[b] ± 0.07
Foraging diversity	0.54[a] ± 0.09	0.65[a] ± 0.10	1.21[b] ± 0.10	0.51[a] ± 0.07	0.79[ab] ± 0.09	1.11[b] ± 0.14
Foraging payoff	0.95[a] ± 0.03	0.98[a] ± 0.03	1.12[b] ± 0.04	1.01 ± 0.03	1.07 ± 0.03	0.97 ± 0.05
Foraging cost	0.18[a] ± 0.05	0.17[a] ± 0.05	0.37[b] ± 0.05	0.14[a] ± 0.04	0.18[a] ± 0.04	0.40[b] ± 0.07
rDWG	0.075 ± 0.010	0.075 ± 0.011	0.080 ± 0.011	0.057[a] ± 0.008	0.056[a] ± 0.009	0.117[b] ± 0.015
Heavy piglets						
Foraging investment	1.04[a] ± 0.04	1.16[a] ± 0.04	1.54[b] ± 0.05	1.18[a] ± 0.05	1.21[ab] ± 0.04	1.35[b] ± 0.04
Foraging diversity	0.54 ± 0.10	0.51 ± 0.10	0.69 ± 0.11	0.39 ± 0.11	0.75 ± 0.10	0.59 ± 0.09
Foraging payoff	0.95[a] ± 0.04	1.05[a] ± 0.04	1.26[b] ± 0.04	1.09 ± 0.05	1.03 ± 0.04	1.14 ± 0.04
Foraging cost	0.09[a] ± 0.03	0.11[a] ± 0.03	0.29[b] ± 0.03	0.09[a] ± 0.04	0.18[ab] ± 0.03	0.21[b] ± 0.03
rDWG	0.088 ± 0.012	0.057 ± 0.012	0.063 ± 0.013	0.056 ± 0.013	0.062 ± 0.012	0.091 ± 0.011

rBW, relative body weight (low <0.95, medium 0.95–1.08, high >1.08); BWcv, within-litter body weight variability.

[a,b,c] Different letters indicate significantly (P < 0.05) different least square means for TA and BWcv.

weight, but positively affects growth performance only in littermates of low body weight.

The present findings are in accordance with the simplistic game theory model of suckling behavior in polytocous mammals recently proposed by Skok (2018). This model, which includes only simple rules of monopolization and sharing of a limited resource (suckling positions), proposed that more specialized, strictly oriented suckling behavior results in a relatively higher foraging payoff (our results exposed growth rate instead) for the weakest littermates, but not for neonates of medium or high body weight. This implies that, in polytocous mammals where neonates establish a well-defined social order (suckling order is considered the first social order), specializing in a particular suckling position is a beneficial strategy for weaker (light) neonates, leading to the hypothesis that physically weaker neonates may have driven the evolution of neonatal foraging specialization in terms of positioning on the mother's udder. However, thesis deployment should consider the mother–offspring system as a whole including also a disagreement over maternal investment and offspring demands, termed mother–offspring conflict (Trivers 1974). According to the model of Stockley and Parker (2002), a mother's survival decreases with increasing total mass of the litter. In this regard, maternal care is normally diminished by too-high offspring demands (Bateson 1994) that are largely dependent on offspring body weight. Heavier neonates exert stronger pressure on the mother as they require a higher maternal investment (Lee et al. 1991; Ocepek et al. 2016). In the early stages of lactation, therefore, the mother can easily meet the needs of her offspring (Bateson 1994) and shows no avoidance behavior or aggression toward the infants; however, the mother's responses to offspring demands become gradually more rigorous during lactation (Trivers 1974). In the pig, for example, instances of shortening and termination of nursing induced by the mother increase progressively during the course of lactation (Valros et al. 2002). However, offspring demands on maternal milk (and care in general) decrease with age when offspring *inter alia* begin to consume solid food instead of milk. Ultimately, neonatal body weight appears to be an important

factor determining the time of weaning onset, with heavier juveniles being weaned earlier, at least in ungulates and primates (Lee et al. 1991). Together with our results showing foraging specialization (suckling order) as being beneficial exclusively for weaklings, that is, littermates with low body weight, this may indirectly indicate that producing litters containing more low-weight (but viable) siblings was evolutionarily favored in species with a well-defined suckling order. Litters with a higher proportion of smaller but viable individuals may suckle more regularly and thus have a higher chance of surviving, whereas litters where large and more demanding individuals predominate are more frequently deprived of access to the udder due to maternal avoidance behavior. Indeed, producing litters with a higher proportion of small individuals could also be a consequence of the evolution of larger litters, considering the apparent trade-off between litter size and body weight in eutherian mammals (Read and Harvey 1989). It may follow that evolution of suckling order may have co-evolved with maternal optimization of investment in offspring against their demands, which has already been indicated for polytocous mammals (Skok 2018). Thus, producing neonates of smaller body size, which are inclined to foraging specialization to increase their own survival, presumably ensure an optimal balance between the survival of the offspring/mother, and further reproduction.
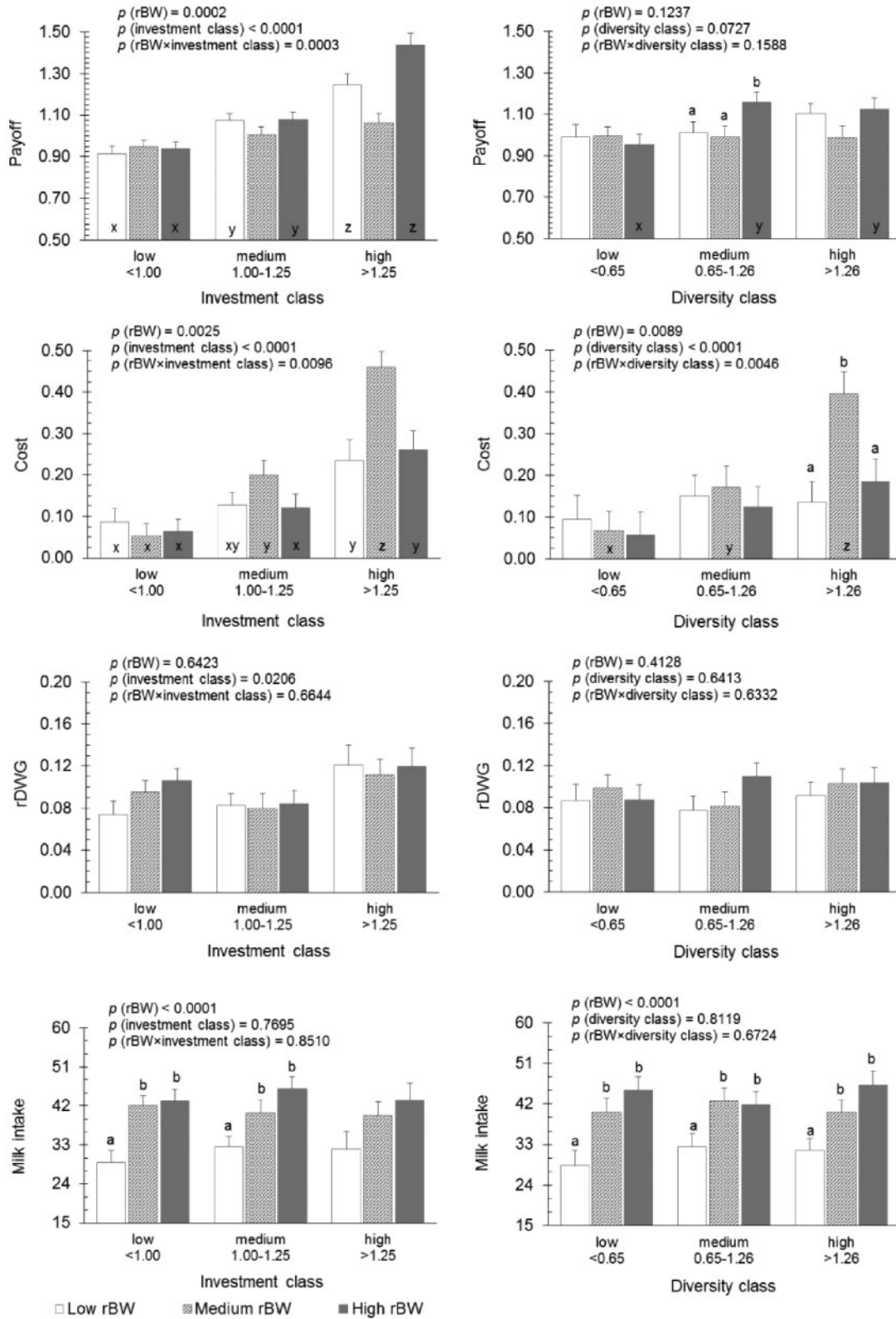
Figure 3. Effect of different suckling strategies on foraging payoff, foraging cost, growth rate, and milk intake in whole lactation period (Analysis 2).
rBW, relative body weight (low <0.95, medium 0.95–1.13, high >1.13).
[abc]Different letters indicate significantly ($P < 0.05$) different least square means for rBW classes within each foraging investment (or diversity) class.
[xyz]Different letters indicate significantly ($P < 0.05$) different least square means for foraging investment (or diversity) class within each rBW class.

Conflict of Interest

The authors declare that there is no conflict of interest.

Authors' Contributions

J.S. contributed to conception or design of the work, data collection, data analysis and interpretation, and drafting of the article; M.P.P. contributed to data analysis, interpretation, and drafting of the article.

References

Bateson P, 1994. The dynamics of parent-offspring relationships in mammals. *Trends Ecol Evol* 9:399–403.

Bolnick DI, Svanbäck R, Fordyce JA, Yang LH, Davis JM et al. 2003. The ecology of individuals: incidence and implications of individual specialization. *Am Nat* 161:1–28.

Brown JH, Maurer BA, 1986. Body size, ecological dominance and Cope's rule. *Nature* 324:248–250.

Cloyed CS, Eason PK, 2017. Niche partitioning and the role of intraspecific niche variation in structuring a guild of generalist anurans. *R Soc Open Sci* 4:170060.

De Passillé AMB, Rushen J, Hartsock TG, 1988. Ontogeny of teat fidelity in pigs and its relation to competition at suckling. *Can J Anim Sci* 68: 325–338.

Drake A, Fraser D, Weary DM, 2008. Parent - offspring resource allocation in domestic pigs. *Behav Ecol Sociobiol* 62:309–319.

Drickamer LC, Vandenbergh JG, Colby DR, 1973. Predictors of dominance in the male golden hamster *Mesocricetus auratus*. *Anim Behav* 21:557–563.

Gall GE, Manser MB, 2018. Spatial structure of foraging meerkat groups is affected by both social and ecological factors. *Behav Ecol Sociobiol* 72: 1–9.

Harestad AS, Bunnel FL, 1979. Home range and body weight: a reevaluation. *Ecology* 60:389–402.

Hofer H, Benhaiem S, Golla W, East ML, 2016. Trade-offs in lactation and milk intake by competing siblings in a fluctuating environment. *Behav Ecol* 27:1567–1578.

King RH, Mullan BP, Dunshea FR, Dove H, 1997. The influence of piglet body weight on milk production of sows. *Livest Prod Sci* 47:169–174.

Lee PC, Majluf P, Gordon IJ, 1991. Growth, weaning and maternal investment from a comparative perspective. *J Zool* 225:99–114.

Morgan D, Grant KA, Prioleau OA, Nader SH, Kaplan JR et al. 2000. Predictors of social status in cynomolgus monkeys *Macaca fascicularis* after group formation. *Am J Primatol* 52:115–131.

Ocepek M, Andersen-Ranberg I, Edwards SA, Fredriksen B, Framstad T et al. 2016. Can a super sow be a robust sow? Consequences of litter investment in purebred and crossbred sows of different parities. *J Anim Sci* 94:3550–3560.

Orben RA, Paredes R, Roby DD, Irons DB, Shaffer SA, 2015. Body size affects individual winter foraging strategies of thick-billed murres in the Bering Sea. *J Anim Ecol* 84:1589–1599.

Price SA, Hopkins SS, 2015. The macroevolutionary relationship between diet and body mass across mammals. *Biol J Linnean Soc* 115:173–184.

Puppe B, Tuchscherer A, 1999. Developmental and territorial aspects of suckling behaviour in the domestic pig *Sus scrofa f. domestica*. *J Zool* 249: 307–313.

Read AF, Harvey PH, 1989. Life history differences among the eutherian radiations. *J Zool* 219:329–353.

Riek A, 2008. Relationship between milk energy intake and growth rate in suckling mammalian young at peak lactation: an updated meta-analysis. *J Zool* 274:160–170.

Robertson A, McDonald RA, Delahay RJ, Kelly SD, Bearhop S, 2015. Resource availability affects individual niche variation and its consequences in group-living European badgers *Meles meles*. *Oecologia* 178:31–43.

Rödel HG, Bautista A, García-Torres E, Martínez-Gómez M, Hudson R, 2008. Why do heavy littermates grow better than lighter ones? A study in wild and domestic European rabbits. *Physiol Behav* 95:441–448.

Schoener TW, 1971. Theory of feeding strategies. *Annu Rev Ecol Evol Syst* 2: 369–404.

Schoener TW, 1974. Resource partitioning in ecological communities. *Science* 185:27–39.

Sheppard CE, Inger R, McDonald RA, Barker S, Jackson AL et al. 2018. Intragroup competition predicts individual foraging specialisation in a group-living mammal. *Ecol Lett* 21:665–673.

Skok J, 2018. On the presence and absence of suckling order in polytocous mammals. *Behav Process* 148:10–15.

Skok J, Gerken M, 2016. Suckling strategies in the pig: the Göttingen minipig as a model. *Lives Sci* 184:78–84.

Skok J, Škorjanc D, 2014. Fighting during suckling: is it really an epiphenomenon? *Ethology* 120:627–632.

Stockley P, Parker GA, 2002. Life history consequences of mammal sibling rivalry. *Proc Natl Acad Sci USA* 99:12932–12937.

Svanbäck R, Bolnick DI, 2005. Intraspecific competition affects the strength of individual specialization: an optimal diet theory method. *Evol Ecol Res* 7: 993–1012.

Swihart RK, Slade NA, Bergstrom BJ, 1988. Relating body size to the rate of home range use in mammals. *Ecology* 69:393–399.

Trivers RL, 1974. Parent-offspring conflict. *Integr Comp Biol* 14:249–264.

Tucker MA, Ord TJ, Rogers TL, 2014. Evolutionary predictors of mammalian home range size: body mass, diet and the environment. *Glob Ecol Biogeogr* 23:1105–1114.

Valros AE, Rundgren M, Špinka M, Saloniemi H, Rydhmer L et al. 2002. Nursing behaviour of sows during 5 weeks lactation and effects on piglet growth. *Appl Anim Behav Sci* 76:93–104.

Wamberg S, Tauson AH, 1998. Daily milk intake and body water turnover in suckling mink *Mustela vison* kits1. *Comp Biochem Physiol A Mol Integr Physiol* 119:931–939.

Wauters L, Dhondt AA, 1989. Body weight, longevity and reproductive success in red squirrels *Sciurus vulgaris*. *J Anim Ecol* 58:637–651.

Weise MJ, Harvey JT, Costa DP, 2010. The role of body size in individual-based foraging strategies of a top marine predator. *Ecology* 91:1004–1015.