



Begging for Milk: Evolution of Teat Massaging in Suckling Pigs

I. DOSTÁLKOVÁ*[†], M. ŠPINKA[‡] AND P. KINDLMANN*

**Faculty of Biological Sciences, University of South Bohemia, Czech Academy of Sciences, Branišovská 31, CZ 37005 České Budějovice, Czech Republic and* [‡]*Ethology Group, Research Institute of Animal Production, CZ 140 00 Prague - Uhřetěves, Czech Republic*

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We present a model that simulates the evolution of teat massaging (begging) by suckling piglets (*Sus scrofa*) and milk distribution among teats (provisioning) by their mothers. Contrary to previous begging models, this one incorporates an ontogenetic dimension in that the inherited begging and provisioning rules are repeatedly allowed to interact, and their consequences for milk intake, growth and death probability are assessed, during each nursing. We test the model under three selection regimes differing in the relative importance of the between-litter selection component. We show that the selection regime with the strongest between-litter selection component leads to lowest begging levels and most effective milk utilization, thus supporting the hypothesis that selection based on whole litters may attenuate sibling competition.

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Introduction

Food solicitation (“begging”) by young animals, which induces changes in parental provisioning behaviour is common among altricial birds (e. g. Redondo & Castro, 1992; Price & Ydenberg, 1995; Lotem, 1998; Leonard & Horn, 2001). Evolutionary interactions between the “begging” function (level of solicitation), $x(c)$, of a young in condition, c , and the “provisioning” function, $y(x)$, describing the amount of food supplied by a parent in response to begging level, x , result in a “parent–offspring conflict”: offspring demanding more resources than it is optimal for the parent to provide (Trivers, 1974; Godfray, 1995). In the clutches of more than one young, there is also “sibling competition” with each offspring striving to get a larger

share than its nestmates (Mock & Parker, 1998). In many mammalian species, a large part of teat manipulation during nursing is non-nutritive (Hall & Williams, 1983; Lidfors *et al.*, 1994; Špinka & Algers, 1995; de Passillé & Rushen, 1997). This manipulation affects milk release (Wakerley *et al.*, 1988; Bruckmeier, 2001) and possibly also milk production (Jensen *et al.*, 1988; Svennersten, 1992; Jung, 2001), which enables a tactile form of begging to evolve. Yet, this form of food solicitation has been much less investigated than the visual and acoustic signalling of young birds to their parents.

If the fitness of an offspring $f(c, x, y)$, depends on condition c of the young, its begging level x and food received from the parent, y , while the residual fitness of the parent $g(y)$ depends only on y , then there exists an evolutionary stable strategy, i.e. a pair of functions $x^*(c)$ and $y^*(x)$ such that any modification of either of them will

[†] Author to whom correspondence should be addressed.
E-mail: dost@tix.bf.jcu.cz

be selected against. At this “signalling equilibrium”, young in lower condition beg more and parents provide more food in response to higher begging (Godfray, 1991). Thus, begging carries an “honest” information about the need of an individual young and parents use it to allocate care more efficiently. Yet, because of the sibling competition, this honesty is only achieved at a cost: the begging itself consumes a substantial part of the provided food. If the parental response $y(x)$ is fixed and the begging $x(y)$ depends on the current provisioning rather than on the long-term condition, then the “scramble competition” model applies (Parker & Macnair, 1979; Mock & Parker, 1998). The model suggests that even higher levels of competitive begging will evolve especially in large broods, which may substantially reduce parental fitness.

The above-mentioned analytical models—in order to be tractable—do not incorporate many factors typical for realistic parent–offspring interactions in natural populations, like feeding frequency, typical growth curves and mortality rates, mutual interactions between siblings, food conversion efficiency and learning abilities. Numerical models have shown that these might influence the begging/provisioning interaction. For example, Rodríguez-Gironés *et al.*, (1998) have shown that Godfray’s (Godfray, 1991) “signalling” equilibrium is unstable under realistic conditions and populations slide into a second, “non-signalling” Nash equilibrium with zero begging level. One important aspect that has been ignored up till now is that interactions of $x(c)$ and $y(x)$ occur more than once within each generation, as young are usually fed several hundred times before fledging or weaning (Redondo & Castro, 1992). To our knowledge, neither a model, nor a simulation of the offspring begging/parental provisioning co-evolution assuming its dynamics during ontogenesis has ever been published.

Here, we fill this gap by developing a model that simulates the evolution of teat massaging (begging) by suckling litters of piglets (*Sus scrofa*) and milk distribution among teats (provisioning) by their mothers. *Sus scrofa* was chosen as a model species, because understanding the evolution of “begging-through-teat-massaging” has a potential practical application.

In the herds of domestic pigs, the selection of new breeding females among the young animals occurs according to different criteria, including litter size at weaning, litter weight at weaning and individual growth performance. The breeding programmes thus put artificial selection pressures on the amount of milk that the mother gives to her progeny and on the distribution of the milk. The pattern of milk provisioning, in turn, may significantly depend on teat massaging (see below), and understanding the co-evolution of teat massaging and milk provisioning is thus important for our ability to predict the outcomes of breeding programmes.

We test our model under three selection regimes, which differ in the relative strength of the “individual selection” vs. “group selection” components. That is, in one of the regimes the selection of animals, which will be bred in the next generation, was based on individual piglets whereas in the other two it was based partly or fully on the condition of whole litters. It has been suggested for animals that live in stable groups and compete for a limited resource that positive selection for individual performance trait (such as growth) can have a negative effect on the mean performance in the population (Muir, 1997). This is because the increase in the performance of the individual has, through competitive behaviour, a negative influence on the performance of its group mates. Viewing this from the opposite perspective, selection at the group level should decrease competitive behaviour. Thus, one can assume that in stable-group-living animals with restricted resources, group-based selection will result in larger and/or faster increase in the mean performance than selection based on individuals (Wilson, 1997). Empirical evidence supporting this hypothesis has been found for *Tribolium castaneum* (Wade, 1997) and domestic laying hens (Craig & Muir, 1996; Muir, 1997). For litters of mammalian young, this hypothesis specifically predicts that between-litter selection for performance traits like weaning litter size or weaning litter weight may act against sibling competition, attenuate begging and other competitive behaviour and improve the utilization of the resource, i.e. the milk. Assuming that begging-through-teat-massaging is a competitive behaviour, we test

this hypothesis here: we test, whether regimes with stronger between-litter selection component will lead to lower begging intensity and more effective milk utilization. We assess our predictions by addressing the following questions:

(i) How will evolution shape the begging and milking functions and will they differ between the selection regimes?

(ii) How efficiently will energy contained in milk be used for piglet growth under the three regimes? Which proportion of milk will be converted into biomass of piglets that survived until weaning as opposed to that spent on begging and/or invested in piglets that died before weaning?

(iii) How will mortality and average piglet weaning weight develop under the three regimes?

Biological Background—Suckling in the Pig

Female pigs give birth to litters of 3–8 (wild boar, Mohr, 1960) or 6–14 (European domestic breeds) piglets that each weigh over 1 kg at birth. Within the first 1–3 days of life, each piglet forms an attachment to one teat of its mother and sucks almost exclusively from that teat until weaning (Rossillon-Warnier & Paquay, 1984; de Passillé *et al.*, 1988; Puppe & Tuchscherer, 1999). Piglets are nursed in about 1 hr intervals during distinct nursing periods lasting several minutes, but the actual milk intake occurs only during 15–20 s of milk ejection period in the middle of nursing (Fraser, 1980). During the rest of the nursing period each piglet noses, rubs and (non-nutritively) sucks its own teat. The intensity and duration of this teat massage (“begging behaviour”) is enhanced if the piglets are hungry or are gaining weight too slowly (Špinka & Algers, 1995). There is some evidence that a more intensive massage increases the amount of milk received in future nursings (Špinka & Algers, 1995; Jensen *et al.*, 1998), although it is unclear as to whether the effect is central or local. Massaging consumes extra energy since piglets lose weight at a faster rate during the non-nutritive phase of the nursing than when resting (Klaver *et al.*, 1981; Noblet & Etienne, 1986). Piglets suffer large pre-weaning mortality (10–25% in domestic herds) during the first days

of life (Daza *et al.*, 1999; Herpin *et al.*, 2001). The low-weight piglets are at a much higher risk (Weary *et al.*, 1998; Marchant *et al.*, 2000; Roehe & Kalm, 2000) and this early loss of low-prospect progeny may be a case of adaptive litter size reduction (Forbes, 1993; Fraser *et al.*, 1995). In European domestic herds, weaning is most frequently imposed between Day 21 and Day 35 post-partum. Different criteria are applied for selecting new breeding animals, depending on the main purpose of the herd, e.g. whether replacement animals are raised within the herd or purchased from outside, whether the herd sells breeding animals or just animals for slaughter, whether the main purpose of the selection is genetic improvement in fertility or in growth rates.

The Model

We simulated the evolution of the begging and provisioning functions. Begging function, B , was assumed to be the level of udder massage each piglet performs, dependent on its weight, relative to its littermates. Provisioning or “milking” function, M , was assumed to be the amount of milk that the mother releases to individual piglets in response to their relative levels of “begging”. The basic model structure is shown in Fig. 1 and its parameters in Table 1.

We simulated a series of k hypothetical breeding generations. Each generation consisted of N animals (sows), each having n offspring (only female offspring were considered). Litter size at birth, nursing frequency, the total amount of milk given per nursing and mortality were assumed to be the same in all animals and generations. We arbitrarily assumed 11 relative weight categories of the piglets at each instant.

Each individual, I , (both sow and piglet) was characterized by its birth weight, $W(0)$, and two 11-dimensional vectors, \mathbf{B} and \mathbf{M} : $I = I(W(0), \mathbf{B}, \mathbf{M}) = (W(0), (B(1), B(2), \dots, B(11)), (M(1), M(2), \dots, M(11)))$. Here $B(i)$ is the intensity of begging, provided that the individual belongs to the i -th weight category and $M(i)$ is the relative amount of milk that this individual provides as a response to begging of an offspring belonging—from this individual’s point of view—to category i . These vectors represented the begging

and provisioning functions, which were “inherited” and “evolving” in a way described below. The weight of each suckling piglet, $W(t)$, was assumed to be a function of time, t .

The structure of the simulations is shown in Fig. 1. They consisted of a set of nested computer procedures. The main one, called

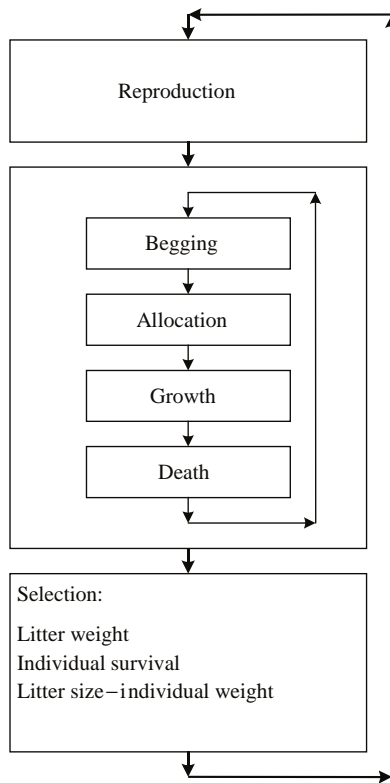


FIG. 1. Flow diagram describing the basic structure of the model.

Evolution, consisted of repetitive usage of procedures *Reproduction*, *Life* and *Selection*. Procedure *Life* simulated the processes from birth to weaning in each sow and her litter—growth of piglets, their begging and milking by the sow. Procedure *Selection* simulated the process of selection of a new generation of sows from the offspring of the previous generation of sows. Finally, procedure *Reproduction* simulated the process, in which a piglet selected for further breeding will give birth to her offspring—thus it described the weights and inherited characteristics (begging and provisioning functions) of each of her offspring. The initial values used in the model are defined in Table 1. We now describe each of these procedures.

Procedure Reproduction: We arbitrarily assumed that each mother gives birth to n piglets, I_i , $i=1, 2, \dots, n$, each with its own characteristics, $I_i = I_i(W_i(0), \mathbf{B}_i, \mathbf{M}_i)$. The birth size, $W_i(0)$, was chosen from a normal distribution (see Table 1 for parameters). Components of vectors \mathbf{B}_i and \mathbf{M}_i were defined as

$$B_i(i) = B(i) + R_b B_{var}(1 - |I - r_b|/10),$$

$$M_i(i) = M(i) + R_m M_{var}(1 - |I - r_m|/10),$$

where B_{var} and M_{var} are parameters, r_b and r_m were integers chosen from a uniform distribution in the interval $\langle 0; 11 \rangle$ and R_b and R_m were chosen from the normal $N(0,1)$ distribution.

TABLE 1
Parameters used in the model

Parameter	Notation	Type	Constant value	Initial value
Number of mothers	N	Constant	10	—
Litter size at parturition	N	Constant	8	—
Piglet birth weight mean	$W_0(0)$	Constant	1.5 kg	—
Piglet birth weight variation	—	Constant	3 variance	—
Begging	\mathbf{B}	Evolving	—	0.002 for all 11 weight categories
Milking	\mathbf{M}	Evolving	—	0.004*k, $k=0,1, \dots, 10$ k is category
Heritability of begging	$1/B_{var}$	Constant	60	—
Heritability of milking	$1/M_{var}$	Constant	90	—
Number of nursings until weaning	K	Constant	600	—
Milk per nursing	k_T	Constant	0.2 kg	—
Milk to body weight conversion	C	Constant	0.2	—
Probability of death	P	Dependent on weight	—	—
Number of generations	Iter	Constant	100	—

Thus the values of $B_i(i)$ and $M_i(i)$ were similar to those of the parent—they were “inherited”, and the begging and provisioning functions differed from those of the parents in that at a randomly chosen category (defined by r_b and r_m), they were “disturbed” and this “disturbance” faded out with the distance from this category. The sizes of the disturbance were random, but their means were proportional to B_{var} and M_{var} —thus the inverses of these parameters might be considered as a measure of “heritability” of the begging and provisioning functions.

Procedure Begging: At any instant and within each litter, piglets were categorized into 11 categories according to their weight relative to their sibs. The category, $c(t, i)$, of i -th piglet at time t was defined as

$$c(t, i) = 5 + int \left[20 \left(\frac{W_i(t)}{\sum_{j=1}^n W_j(t)/n} - 1 \right) \right]$$

with additional conditions: if $c(t, i) > 10$, then $c(t, i) = 10$ and if $c(t, i) < 0$, then $c(t, i) = 0$, where $W_i(t)$ is the weight of i -th piglet in the litter of total size n piglets (see Table 2). The energy spent by begging of this piglet, was then set equal to $B(c(t, i))$.

Thus, piglets with less than 75% of average body weight were put into category 0, piglets with 125% and larger weight into category 10, piglets with average weight into category 5, etc. (Table 2). Thus, this procedure determines the

TABLE 2
Range of the weight categories

Category	$\frac{W_i(t)}{\sum_{j=1}^n W_j(t)/n}$
0	$(-\infty, 0.75 >$
1	$(0.75, 0.8 >$
2	$(0.8, 0.85 >$
3	$(0.85, 0.9 >$
4	$(0.9, 0.95 >$
5	$(0.95, 1.05 >$
6	$< 1.05, 1.1 >$
7	$< 1.1, 1.15 >$
8	$< 1.15, 1.2 >$
9	$< 1.2, 1.25 >$
10	$< 1.25, + \infty >$

begging intensity that the piglet exerts as a function of its own weight, relative to its sibs, and to its inherited “strategy” for begging—the value $B(i)$. While begging and provisioning functions are “inherited” and fixed during juvenile life, the category of the piglet is determined at each time step and therefore may change according to how it grows relative to its sibs.

Procedure Allocation: Similar to weight categories, at any instant and within each litter, begging of piglets was also categorized into 11 categories. The category, $b(t, i)$, of begging of i -th piglet at time t was defined as

$$b(t, i) = 5 + int \left[20 \left(\frac{B_i(t)}{\sum_{j=1}^n B_j(t)/n} - 1 \right) \right]$$

with additional conditions: if $b(t, i) > 10$, then $b(t, i) = 10$ and if $b(t, i) < 0$, then $b(t, i) = 0$. As the begging functions $B(i)$ were not necessarily directly proportional to i , begging of a piglet did not necessarily correspond to its weight category. Each piglet was then allocated the amount of energy $M_{al}(t, i)$ contained in milk, which made up the proportion $M(b(t, i))$ of the total amount of milk, k_T , offered by the sow to her litter during one nursing:

$$M_{al}(t, i) = k_T \frac{M(b(t, i))}{\sum_{j=1}^n M(b(t, j))}$$

Procedure Growth: The growth of piglets from birth to weaning was modelled as

$$W(t + 1) = W(t) + c(M_{al}(t) - B(t)),$$

where the time unit was equal to one between-nursing interval and c is the energy to body weight conversion ratio. Thus, the increment in weight per unit time was assumed to be proportional to the difference between the energy gained from milk and energy spent by begging.

Procedure Death: At each instant, each piglet was assumed to die with the probability

$$P = max(0; 1 - A(W_i(t) - 0.5)^B),$$

where A and B are constants, in the model we used $A = 0.97, B = 0.07$.

Thus, the probability of the death of a piglet at any instant was negatively correlated with its weight, and transformed into biological meaning which means that piglets below 0.5 kg died immediately, whereas once they reached more than 2.1 kg, they always survived. This simulated the significant offspring mortality—especially of the relatively weaker ones—immediately after birth observed in reality.

Procedure Life: The fate of all the offspring of each mother was followed by iterating procedures *Begging*, *Allocation*, *Growth* and *Death* for 600 time steps, simulating the suckling period (20 nursing events per day, 30 days from birth to weaning).

Procedure Selection: New breeding generation of N mothers was selected from the offspring that were alive at the end of the *Life* procedure according to one of the following three selection procedures:

“*Individual Survival*” selection (*IS*). The new set of mothers was chosen at random from the set of all piglets alive at weaning. That is, begging only influenced the piglet’s chance to stay alive until weaning, but not its later fate. This selection regime may somewhat resemble the natural selection since pigs in their first months of life are known to have a high ability of compensatory growth (Valaja *et al.*, 1992) and therefore individuals surviving to weaning, even if lighter than their siblings, can catch up the same weight before the critical winter season, when the mortality starts to increase again (Mohr, 1960, p. 35). Since there was no selection based on whole litters, we predicted that this regime will result in highest levels of begging and poorest milk utilization.

“*Litter Weight*” selection (*LW*). The new set of mothers was chosen at random only from the offspring of the three mothers, which produced the largest mass of living piglets at weaning. This does not simulate a specific selection regime, but reflects that in artificial breeding the total weight of the weaned piglets is sometimes taken into account. Since the most important selection criterion was based on whole litters, we predicted that begging will be lowest and milk utilization most efficient under this regime.

“*Litter Size–Individual Weight*” selection (*LS–IW*). Ten heaviest piglets from three most

numerous litters at weaning lumped together were chosen as the new set of mothers. This scenario resembles the selection regime in maternal lines of domestic pigs, where litter size is the primary and individual growth the secondary criterion. This regime combined between- and within-litter selection criteria and therefore was predicted to be intermediate in terms of begging level and milk utilization.

Procedure Evolution: For each selection regime, we performed 20 independent replicates of 100 iterations of the sequence of procedures *Reproduction*, *Life* and *Selection*, thus simulating the evolution of life history parameters B and M for 100 generations.

MODEL PARAMETERS (TABLE 1)

Litter size at parturition, piglet birth weight, amount of milk provided per nursing, energy to body weight conversion ratio, number of nursing events until weaning, initial begging level as related to its energy costs and the linearly increasing milking function (Table 1) were derived from realistic values in the *Sus scrofa* species (Jensen, 1988; Rushen & Fraser, 1989; Whittemore, 1993; Špinková *et al.*, 1997; Jensen *et al.*, 1998). The mutation pressure (heritability level) of the begging and the milking function were determined by means of pilot simulations, so that these values enabled the begging and the milking functions to evolve and yet avoided erratic patterns due to excessive randomness in the system caused by low heritability. The number of mothers and number of generations were limited by the computer power available.

STATISTICAL ANALYSIS

In each of the scenarios, for all sows in the last ten generations, the following values were calculated and averaged over the ten generations, all breeding animals considered and all replicates:

- (1) Begging and milking functions for each category.
- (2) Cumulative. Proportions of milk:
 - (i) utilized for body weight increase by piglets that survived until weaning;

- (ii) “wasted” for body weight increase by piglets that died before weaning;
 - (iii) “spent” by any of the piglets as energy needed for begging.
- (3) Numbers of piglets that died before weaning (mortality).
- (4) Average weaning weight of a piglet in the litter.

For each of the variables above, results for different selection regimes were compared by means of a one-way ANOVA followed by the Scheffé’s test multiple comparisons test. The percentage data were arcsine transformed prior to the analysis.

Results

BEGGING AND MILKING FUNCTIONS

Figure 2 shows that evolution under the LW selection regime resulted in a low and very flat begging function. In the LS-IW and the IS scenarios, the begging function increased substantially during the evolution in all weight categories, had a single peak in mid-weight categories and the differences between categories were larger than in the case of the LW selection. One-way ANOVA and subsequent Scheffé’s test confirmed that in all weight categories, begging under the LW regime was lower than under either of the LS-IW and IS regimes (Table 3), whereas there were no significant differences between the latter two regimes.

Although the shapes of the milking function seem to be different for the LS-IW and the IS scenario (Fig. 3), the differences were not

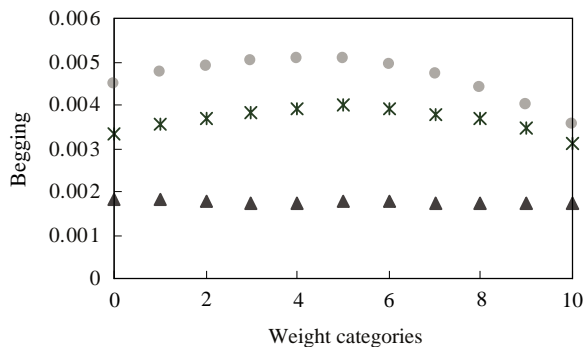


FIG. 2. Average begging function in the 100-th generation: (▲) LW; (✱) IS; (●) LS-IW.

TABLE 3
Comparison of scenarios for each weight category

Weight category	LW × IS	IS × LS-IW	LW × LS-IW
0	LW < IS*	NS	LW < IS-IW***
1	LW < IS*	NS	LW < IS-IW***
2	LW < IS*	NS	LW < IS-IW***
3	LW < IS*	NS	LW < IS-IW***
4	LW < IS*	NS	LW < IS-IW***
5	LW < IS*	NS	LW < IS-IW***
6	LW < IS*	NS	LW < IS-IW***
7	LW < IS*	NS	LW < IS-IW***
8	LW < IS*	NS	LW < IS-IW***
9	LW < IS*	NS	LW < IS-IW***
10	LW < IS*	NS	LW < IS-IW***

Note: Levels of statistical significance used in the table: NS: $p \geq 0.05$; *: $p < 0.05$; **: $p < 0.01$; ***: $p < 0.001$. The relations between factor levels resulting from the multiple comparison tests are denoted by < or >

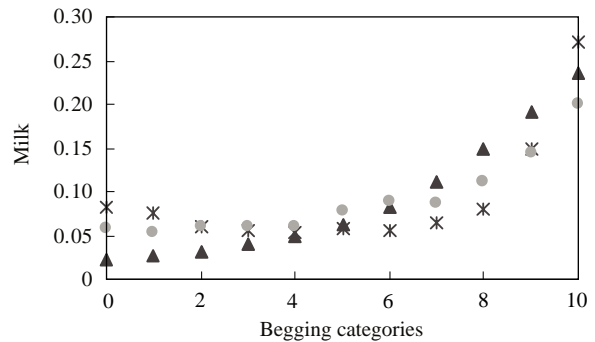


FIG. 3. Average milking function in the 100-th generation: (▲) LW; (✱) IS; (●) LS-IW.

significant except for begging categories 6 and 8 (Table 4). More pronounced differences appeared between the milking function in the LW scenario and in the other two scenarios. In categories 0–3, LW milking was lower and in categories 7–9 higher than in the LS-IW or IS regimes (Table 4).

ENERGY ALLOCATION

The proportion of energy spent by begging was similar (about 5%) in all three scenarios in the first generations, but then developed differently [Fig. 4(a)]. In the LW scenario, it steadily decreased and in the IS scenario it increased throughout the evolution. In the LS-IW scenario, begging increased steeply

TABLE 4
Comparison of scenarios for each milk category

Milk category	LW × IS	IS × LS-IW	LW × LS-IW
0	LW < IS*	NS	NS
1	LW < IS*	NS	NS
2	LW < IS*	NS	LW < LS-IW*
3	NS	NS	LW < LS-IW*
4	NS	NS	NS
5	NS	NS	NS
6	NS	IS < LS-IW*	NS
7	LW > IS***	NS	LW > LS-IW*
8	LW > IS***	IS < LS-IW*	LW > LS-IW*
9	LW > IS*	NS	LW > LS-IW*
10	NS	NS	NS

Note: Levels of statistical significance used in the table: NS: $p \geq 0.05$; *: $p < 0.05$; **: $p < 0.01$; ***: $p < 0.001$. The relations between factor levels resulting from the multiple comparison tests are denoted by < or >.

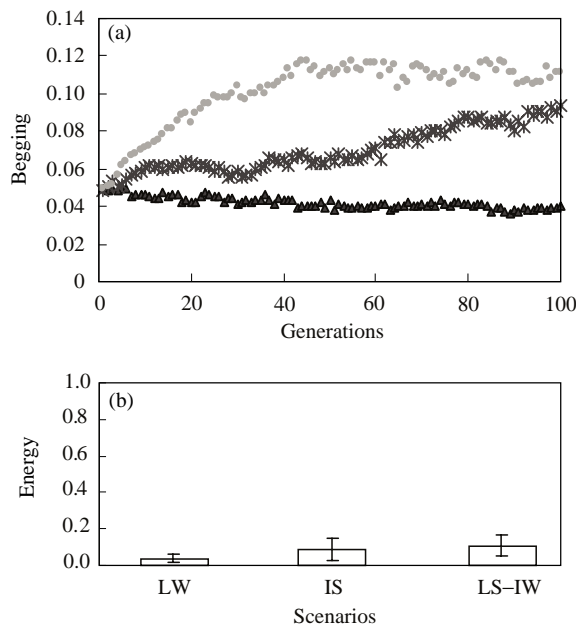


FIG. 4. Average proportions of milk (expressed as energy) spent in begging: (a) during the evolution cycle, (b) at 90-th – 100-th generations. The bars defining the mean value of each scenario are completed by estimates of the standard deviations: (▲) LW; (×) IS; (●) LS-IW.

during the first 50 generations and then levelled off. At the 90-th-100-th generation, begging consumed more energy (about 10%) in the LS-IW and the IS scenarios than in the LW scenario [around 4%; Fig. 4(b)]. At this point, the LS-IW and the IS scenarios did not differ from each other [Fig. 4(b)].

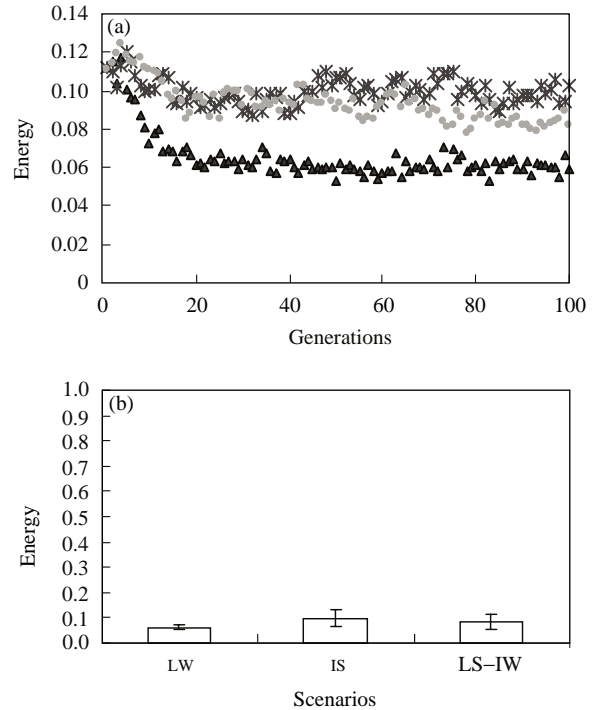


FIG. 5. Average proportions of milk wasted by dead piglets: (a) during the evolution cycle, (b) at 90-th – 100-th generations. The bars defining the mean value of each scenario are completed by estimates of the standard deviations: (▲) LW; (×) IS; (●) LS-IW.

The proportion of milk “wasted” by feeding milk to piglets which eventually died was equal to about 11% at the beginning of evolution [Fig. 5(a)]. It decreased quickly during the first 20 generations in the LW scenario and levelled off after that. Under both LS-IW and IS regimes, the decrease was slower and ultimately approached significantly higher values than in the LW scenario [Fig. 5(b)].

The proportion of milk utilized in the growth of piglets, which survived until weaning started at about 84%. Under the LW regime, it increased during the first 20 generations and then remained constant at about 90%. Both in the LS-IW and the IS scenarios, it ended at significantly lower values [Fig. 6(b)], but its evolution was different [Fig. 6(a)].

PIGLET MORTALITY AND GROWTH

The mean number of piglets which died before weaning in the 90-th-100-th generation (mortality) was highest in the LW and lowest in the IS

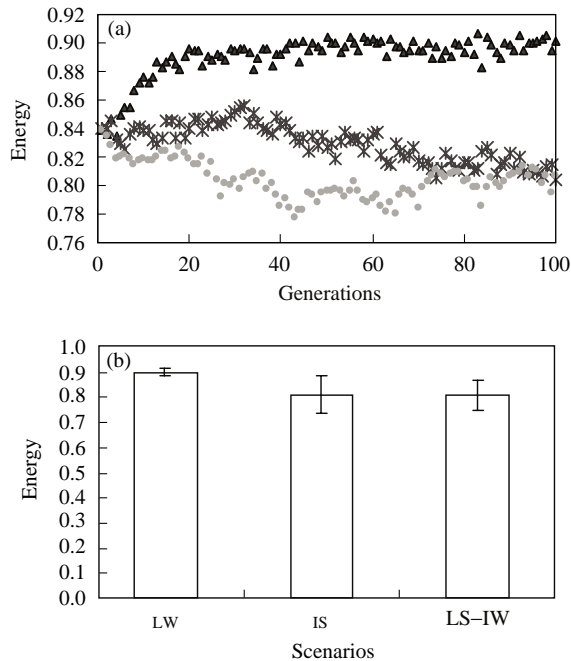


FIG. 6. Average proportions of milk utilized in the growth of piglets: (a) during the evolution cycle, (b) at 90-th – 100-th generations. The bars defining the mean value of each scenario are completed by estimates of the standard deviations: (▲) LW; (×) IS; (●) LS-IW.

scenario [Fig. 7(a) and (b)]. The average piglet weight at weaning in the 90-th–100-th generation was highest in the LW scenario [Fig. 8(a) and (b)].

Discussion

Under the LW regime, simulations resulted in low begging, which consumed less energy and milk was more efficiently utilized for piglet growth, thus contributing to high litter biomass, which was the selection criterion in this regime. Thus, low within-litter competition lead to a reduction of begging and improved milk utilization. At the 100-th generation, the begging function was very flat—thus begging conveyed no information about the condition of the piglets. This indicates that evolution might ultimately lead here to low or no begging.

The milking function that evolved in the LW regime was steeply increasing and thus providing extremely little milk to piglets, which begged little. As a result, piglet mortality was large, low-weight piglets were eliminated early after birth, therefore

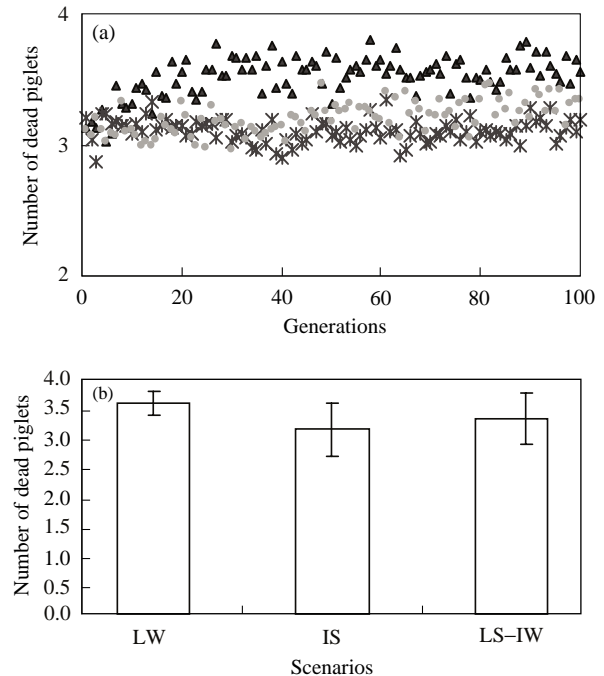


FIG. 7. Mean numbers of piglets dead before weaning: (a) during the evolution cycle, (b) at 90-th – 100-th generations. The bars defining the mean value of each scenario are completed by estimates of the standard deviations: (▲) LW; (×) IS; (●) LS-IW.

more milk was available to the remaining ones, which resulted in largest litter weaning weights.

The LS-IW and the IS regimes resulted in similar begging and milking functions. At the 90-th–100-th generation, begging intensity was high. Piglet begging intensity strongly depended on their relative body weight. Milking function remained to be increasing, i.e. mothers were sensitive to different levels of begging. Milk utilization was lower than in LW because of higher energy expenditure in begging and larger investment into piglets, which eventually died.

In agreement with the hypothesis we tested, begging was lower and milk utilization better in LW than in either IS or LS-IW. However, contrary to what we predicted, evolution did not lead to significantly lower begging and better milk utilization in the LS-IW than in the IS regime. It is not clear, though, whether a simulation that will run for a higher number of generations would not lead to the predicted difference since begging was still increasing and milk utilization decreasing in IS regime at the 100-th generation.

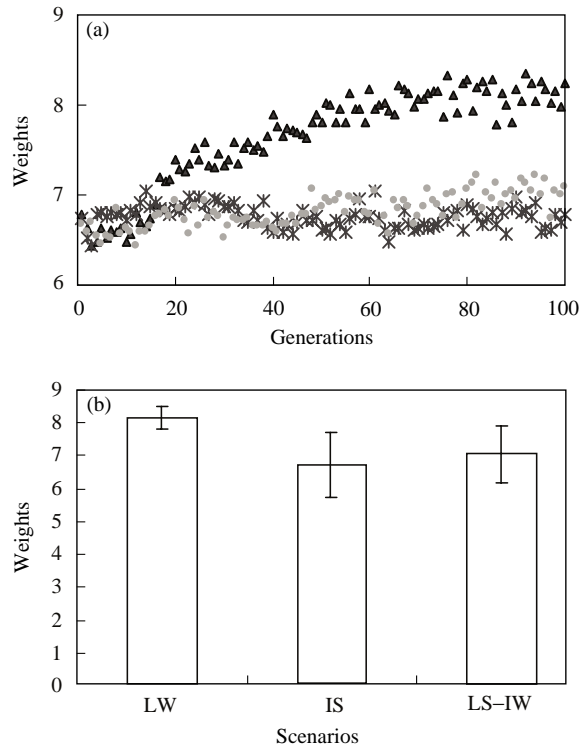


FIG. 8. Average piglet weights at weaning: (a) during the evolution cycle, (b) at 90-th – 100-th generations. The bars defining the mean value of each scenario are completed by estimates of the standard deviations: (▲) LW; (×) IS; (●) LS-IW.

Although the model incorporates an ontogenetic dimension, it is still quite simplistic compared to real ontogenetic and evolutionary complexity and dynamics of the begging/provisioning interaction. The model focuses on the effect of begging on the milk redistribution but does not consider any central mechanisms, i.e. possible effects of udder stimulation on total milk production either via hormonal mechanisms (Rushen *et al.*, 1993; Špinková *et al.*, 1999) or via increasing nursing frequency (Špinková *et al.*, 1997; Auld *et al.*, 2000; Puppe & Tuchscherer, 2000). The model also does not specify the mode of inheritance—it just assumes a certain degree of phenotypic similarity between the mother and her female progeny. Some behavioural traits in pigs are moderately heritable (Hemsworth *et al.*, 1990; McGlone *et al.*, 1991) but no reliable estimates of heritability of teat-massaging or sensitivity to that have been published. The actual magnitude of the effect of teat massaging on milk redistribution has also not yet been well

quantified. Hence, it remains to be seen as to what practical use the model will have in actual breeding programmes for domestic pigs. However, the model can be used, after slight modifications, for exploring the evolution of begging/provisioning behaviour in other species with multiple-young broods or litters, such as many passerine, canid or felid species.

To our knowledge, this is the first model of offspring solicitation/parental provisioning that incorporates both the ontogenetic and the evolutionary time dimension. Further development of this and similar models is opening a new area of research. It enables not only to model evolution more accurately by not neglecting the ontogenetic dynamic of parent–offspring interaction, but it also enables to examine ontogenetic life-history patterns themselves. For instance, once the model converges to an equilibrium, one can examine the ontogenetic distribution of mortality at the equilibrium.

We conclude that

- (i) our model successfully incorporated the ontogenetic dimension into numerical simulations of evolving begging-provisioning interactions,
- (ii) the hypothesis that selection based on the performance of whole litters suppresses competitive begging was partially supported.

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