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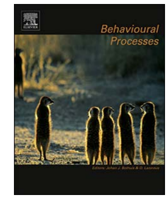

On the presence and absence of suckling order in polytocous mammals

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ABSTRACT

Mammals have developed a variety of suckling behaviours ranging from tenacious nipple attachment in some rodents and marsupials to once-a-day suckling in rabbit. However, a common feature of suckling that was found in many mammals is the suckling order, or a partial preference to suckle a particular teat (teat fidelity) or part of the udder (suckling preference). A lack of suckling order is observed only in a few mammals. In this article, the possible background of the presence or absence of suckling order in eutherian polytocous mammals is discussed either from the maternal investment or sibling competition point of view. Characteristics related to maternal investment in species in which the suckling order has already been studied at least partially, were classified using C4.5 algorithm (J48 classifier in Weka 3.8.1), and decision tree was built. In the context of sibling competition, an extensive form game (game theory) was predicted to show the optimal suckling strategy considering the basic relations among littermates in two situations (littermates of equal strength/dominance and littermates with different strength/dominance). Although no ultimate conclusion can be drawn, it appears that the suckling order is typical for species whose reproductive system requires a lower maternal investment (up to one litter/year, monogamy, biparental care, lower litter birth weight); and, it appears that the suckling order is inherent to the weaker (inferior) siblings.

1. Introduction

Mammalian new-borns are entirely dependent on their mothers for colostrum and milk. The production of milk is energetically expensive for the mothers but indispensable for their offspring. Thus, there is a constant mother-offspring conflict (Trivers, 1974) to establish an investment versus gain balance between a mother and her offspring. On the lines of establishing an optimal investment versus gain balance, a variety of suckling and nursing behaviours have evolved. However, suckling order is a common suckling behaviour observed in most polytocous mammals in which suckling behaviours were studied already. Suckling order is manifested, for example, as teat fidelity (tendency to suckle at the same teat in consecutive sucklings) and teat preference (tendency to suckle at a particular part of mothers' udder), which can operate simultaneously (e.g. in pig; McBride, 1963) or separately, or as tenacious attachment to one nipple observed in some rodents (Gilbert, 1995). The suckling order, either teat fidelity or/and preference, can mitigate the mother-offspring conflict, through optimization of the number of active mammary glands (Benson and Folley, 1957; Griffiths et al., 1972; Kim et al., 2001). The suckling order can also mitigate conflicts in the litter by preventing an excessive competition for teats by siblings and the risk of missing a suckling bout (De Passillé et al., 1988; Hudson et al., 2009).

Only three species of polytocous mammals are known—rabbit (Hudson and Distel, 1983; Bautista et al., 2005), meadow vole (McGuire et al., 2011), and guinea pig (Fey and Trillmich, 2008)—that do not exhibit suckling order, and it appears that their offspring suckle randomly all over the mother's udder.

The mechanisms underlying the presence or absence of suckling order in polytocous mammals, and its role in the reproduction system is still not completely understood, but it can be assumed, that both, mother through her investment in the offspring and offspring through the sibling competition, play a crucial role in the development of certain suckling strategy. Therefore, in the present study, the general characteristics defining maternal investment in polytocous mammals, and its possible relationship to suckling order, were analysed using classification with a decision tree. The suckling strategies were furthermore analysed in the context of sibling competition, using the concept of the game theory. To show the relative nature of choosing a certain suckling strategy, I evaluate pay-offs resulting from decision on the suckling strategy chosen, considering the basic relationships among siblings (strong/dominant vs. weak/inferior).

2. Methods

16 polytocous mammal species, the only species in which the

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Table 1
Sources of data for the analysis.

Species	References
Wild boar (*Sus scrofa*) [a]	McBride (1963), Hemsworth et al. (1976), Horrell, (1997), De Passillé et al. (1988), Fernández-Llario and Mateos-Quesada (2005), Skok and Gerken (2016)
Snow leopard (*Panthera uncia*)	McVittie (1978), Jackson (1996)
Eurasian linx (*Lynx lynx*)	Glukhova and Naidenko (2014), Sunquist and Sunquist (2017)
Mountain lion (*Puma concolor*)	Seidensticker et al. (1973), Pfeifer (1980), Barnhurst and Lindzey (1989)
Rock hyrax (*Procavia johnstoni*)	Hoeck (1977), Hoeck (1982), Barry (1994), Brown and Downs (2005), Downs et al. (2013)
Bush hyrax (*Heterohyrax brucei*)	Hoeck (1977), Hoeck, (1982); Oduor-Okelo et al. (1983), Barry (1994)
Rat (*Rattus norvegicus*)	Bonath (1972), Russell (1980)
Prairie vole (*Microtus ochrogaster*)	McGuire and Novak (1984), Oliveras and Novak (1986), Wang and Novak (1992, Getz et al. (1993), Solomon (1993, McGuire (1998), Hayes and Solomon (2004), McGuire et al. (2011)
Woodland (pine) vole (*Microtus pinetorum*)	FitzGerald and Madison (1983), McGuire and Novak (1984), Oliveras and Novak (1986), McGuire and Sullivan (2001), McGuire et al. (2011)
Meadow vole (*Microtus pennsylvanicus*)	McGuire and Novak (1984), Oliveras and Novak (1986), Wang and Novak (1992), Parker and Lee (2003), McGuire et al. (2011)
Green acouchi (*Myoprocta pratti*)	Kleiman (1970), Kleiman, (1973), Weir, (1971)
Binturong (*Arctictis binturong*)	Schoknecht (1984)
Common marmoset (*Callithrix jacchus*)	Digby (1995), Ximenes and Sousa (1996), Abbott et al. (2003)
Wolf (*Canis lupus*) [a]	Liberg et al. (2005), Arteaga et al. (2013), Hudson et al. (2016)
European rabitt (*Oryctolagus cuniculus*) [a]	Lincoln (1974), Hudson and Distel, (1983), Blasco et al. (1994), Hudson et al. (1996), von Holst et al. (2002); Bautista et al. (2005), Rödel et al. (2009)
Guinea pig (*Cavia porcellus*)	Jouvet-Mounier et al. (1969), Hennessy and Jenkins (1994), Künkele and Trillmich (1997), Fey and Trillmich (2008)
Other data (communal breeding, placenta type)	Hayes (2000), König (2006), Elliot and Crespi (2009)
General data	iucnredlist.org; animaldiversity.org (breeding, mating, young development); genomics.senescence.info/species/(litter size, and body weight – except for green acouchi – Kleiman, 1970, 1973; Weir, 1971)

[a] data on suckling order refers also to its domestic form.

suckling order has already been studied at least partially, were included in the study. Only three species, european rabbit, guinea pig, and meadow vole, lack a suckling order.

Data on suckling behaviour included in the analysis were acquired from previously published work (Google Scholar – searching terms which were used in various combinations: suckling, nursing, behaviour, teat, nipple, order, preference, fidelity, multiparous, polytocous, mammals). Data on general characteristics of species were acquired from *iucnredlist.org* and *animaldiversity.org* (breeding, mating, young development), and *genomics.senescence.info/species/*(litter size and body weight; except for green acouchi – Kleiman, 1970, 1973; Weir, 1971) – see Table 1. Data collected are listed in Table 2; it is important to note, that all data refer to the wild form of a given species, except data on suckling behaviour which mainly sourced from captive animals or domestic form of a given species (see footnotes to Table 1).

2.1. Maternal investment

Attributes (n = 10, Table 2) representing features related to maternal investment were classified using decision tree classifier J48 (C4.5 algorithm), a robust classifier which operates with numeric and nominal attributes, and was implemented in WEKA 3.8.1 (Eibe et al., 2016). C4.5 algorithm considers the information gain ratio and constructs the decision tree with a divide and conquer technique (Ruggieri, 2002); i.e. builds decision trees with choosing the attribute of the data that most effectively splits its set of samples into subsets according to the class value (in our case suckling order), i.e. attribute with the highest normalized information gain (minimal entropy after splitting).

Different combinations of attributes were classified to find most accurate decision tree (highest % of correctly classified instances).

2.2. Sibling competition

Game theory simulator Gambit 15 (McKelvey et al., 2014) was used to evaluate different game strategies/decisions. In an extensive form game with three players, two situations that were predicted had 1) three equal players (theoretical case); and 2) weak (wp), medium (mp), and strong (sp) player (common in the state of nature). Only the most basic game rules (relations) among siblings were included (i.e. without complex relations among siblings, as well as, between siblings and their mother), and were determined as follows:

a) There are three teats (suckling places) predicted;
b) player without suckling order (no-SO) randomly sample teats, while player with suckling order (SO) stick on the same teat and suckle it when free;
c) the stronger player outcompetes the weaker one;
d) players of the same strength share teats evenly;
e) SO player have to share an occupied teat with potential intruders (with the stronger or equal no-SO players), but not more than two third of suckling time on it i.e. pay-offs ranges from 0.33 (e.g. when intruder is stronger player) to 1 (weaker intruder);
f) no-SO player strive to monopolize (suckle alternately) and defend maximum 2 teats at once by taking over a share (if stronger) of a teat, as a priority, not occupied by SO player, and further from weaker/equally strong SO player. For example: if there are no-SO sp and no-SO mp (both striving to monopolize two teats), and SO wp (possessing certain teat), no-SO sp will outcompete both opponents and get maximum pay-off (2 teats), a remaining teat will be shared among no-SO mp and SO wp, however, according to the rule e), only 0.67 suckling pay-off is at disposal for mp, while one third is guaranteed for player with SO, despite its strength.

3. Results

3.1. Maternal investment

According to the decision trees (Fig. 1A, B), the frequency of breeding, mating system, parental care and relative litter birth weight were the attributes that determined the appearance or absence of suckling order. Two decision trees with the same accuracy (93.75% correctly classified instances) were derived from classification. According to the first decision tree (Fig. 1A) species that normally produce only one litter annually as a role exhibited a suckling order, whereas the suckling order in species that produce numerous litters was dependent on the type of mating system − in monogamous species the suckling order was exhibited, while polygamous species lacked suckling order. The second decision tree (Fig. 1B) exposed the type of parental care and