Male lactation: why, why not and is it care?

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Mammals are characterised by their ability to provision offspring with milk, but lactation is normally restricted to females. Why do most males not share this trait? The morphological and physiological modifications necessary for male lactation are possible and, although restrictive, the ecological factors that could select for male lactation seem common enough. Until quite recently, there was no evidence for male lactation in wild mammals, but it has now been reported in two species of Old World fruit bats. Here we review mechanisms that can cause milk production in males and also consider the possibility that male lactation in these bats is a unique adaptive phenomenon.

Introduction

Male parental investment is typically less than that of females, and sometimes far less. Some of this difference is attributable to anisogamy, and is frequently amplified in taxa with postnatal (or posthatching) parental care (see Glossary). This is exemplified by mammals where females not only bear the substantial cost of gestation – in humans a nine-month period of sustained and sizable investment – but they must also engage in the costly act of lactation and suckling of young. This care can last far longer than the gestation period, and the production of milk can be very energetically expensive [1]. Subsequently, females can continue to invest in care during prolonged periods of postweaning learning, where juveniles continue to remain with and be tutored by their mothers. By contrast, a single ejaculate might be all that a male invests, and direct male care occurs in less than 10% of mammal species [2]. Additionally, even when male mammals do provide parental care, their relative effort is usually lower than females, and rarely, if ever, involves milk provisioning [3]. This raises two important questions. First, why is the burden of parental care not shared more evenly by male and female mammals? Second, when male mammals do provide care, why do male and female currencies differ – females lactate but most males do not?

A general answer to the first question was provided by Trivers [4]. He suggested that males never have certainty of paternity, and providing costly care for offspring they did not sire would be selected against. Because strict genetic monogamy is exceedingly rare [5,6], certainty of paternity is frequently low and thus we expect males to care less. While

the impact of paternity on care has been the subject of much debate [2,7,8], the simplest and most general models suggest that Trivers was correct [7], even though other factors such as the adult sex ratio and the intensity of sexual selection on males can also influence male care (Box 1). Additionally, because fertilisation in mammals is internal and requires female investment at least until parturition, males might be able to desert before females – assuming there are benefits to doing so. Therefore, if one parent is likely to evade care, it is more likely to be the male [5].

Nevertheless, there are instances of male care in mammals, humans being a case in point, and some degree of male care is not uncommon in primates, carnivores and perissodactyls. However, as stated above, even in cases where males exhibit care, they usually do not lactate. This absence of lactation by males has been noted [3], but not subjected to as much investigation as the general lack of male parental care [9], and even though the conditions for male care must be met before male lactation could evolve, our focus here is primarily on the lack of male lactation. There are several potential reasons why males do not provide care via lactation, both proximate and ultimate, and we discuss them further below. We also discuss cases of male lactation in the wild in two species of Old World fruit bats. Although it is unclear whether these males actually provide milk to their young, if they do, it raises the interesting question of why they provide care, and why milk? Has adaptive male lactation finally been detected?

Proximate steps to male lactation

While a general lack of male lactation could be due to physiological constraints, the evidence suggests otherwise.

Glossary

Anisogamy: dimorphism in gametes, especially in relation to size.
Certainty of paternity: the average probability that a male is the sire of a given set of offspring.
Extra-pair copulation: any copulation that occurs outside of the social pair.
Extra-pair paternity: offspring sired outside of the social pair.
Lactation: the production of milk to feed offspring; a defining characteristic of mammals.
Parental care: any form of parental behaviour that increases offspring fitness.
Parental investment: any investment by the parent in an individual offspring that increases the survival and reproductive success of that offspring at a cost to the parent's ability to invest in other offspring, or any character or action that increases offspring fitness at a cost to any component of parental fitness.
Pseudopregnancy: a condition resembling pregnancy that occurs in some mammals, sometimes caused by tumours disrupting normal endocrine function, or retention of a corpus luteum following infertile copulation.

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Box 1. Paternity and care

Much has been written about sex biases in care [2,3,7], and our sole aim here is to highlight a simple and therefore very general model showing how certainty of paternity can impact male parental investment [48]. The total reproductive output (r) of each sex must be equal – each offspring has one mother and one father – therefore, the average reproductive output of a male is r divided by the number of males (m), while the average output for females is r divided by the number of females (f). Assume that on average males and females are equally adept at providing a benefit (b) to the offspring and that the unit cost of providing this care (c) is also equal for the sexes – males and females suffer the same time costs, risk and so forth. Cost is the fraction of total reproductive success lost by males and females, cr/m and cr/f, respectively. With this simple framework, we can state that care should evolve when the benefit of parental care exceeds reproductive costs:

$$b > cr/f, \qquad \text{[Equation 1]}$$

which is the same as

$$b > cr/m. \qquad \text{[Equation 2]}$$

Assuming an equal sex ratio – following Fisher's argument [49] – this model does not predict female-biased care, although when one sex is rare, its costs will be greater and hence it will care less. However, when we factor in shared paternity, female care emerges. This occurs because the benefits to males now have to be discounted by the fraction of the offspring sired by other males, $1 - p$. Thus, the equation for males now becomes

$$pb > cr/m, \qquad \text{[Equation 3]}$$

but when the sex ratio is even, obviously the condition for female care to emerge (Equation 1) is easier to meet than it is for males (Equation 3). More recent and expansive sets of models [2] also find negative correlations between care and paternity, although several other factors can influence care. These include the adult sex ratio, the relative intensity of sexual selection on males and the cost of care compared to the costs of mate competition. Feedback loops can also form, and these can dampen or amplify the initial direction of selection [2]. For example, if care is costlier than mate competition, the sex that cares more will be rare, making mate finding for the (initially) less-caring sex more difficult, which should select for the increased care by that sex, reducing sex role divergence [2].

The differentiation of the mammary gland in mammals is similar to that of many other sexually dimorphic traits: in the absence of androgens (male hormones), female characteristics can develop [10]. For example, embryonic testosterone functions as an early inhibitor to nipple formation in rodents [11], and prevents the development of ducts leading to the surface of the nipples. In other species, including primates, development of nipples in males and females is essentially identical until puberty [9]. Thus, androgen suppression at critical stages of mammary gland development could be the first step toward the evolution of mammary function in males.

A second modification involves altering hormones associated with the onset of the mammalian ovarian cycle at puberty. This might not be too problematic, because male and female sex steroids are very similar in structure and the action of testosterone on some target cells necessitates the conversion of testosterone to estrogen via aromatisation [12]. Thus, a mechanism for the synthesis of estrogen already exists in males. If male lactation conferred a fitness benefit, it seems possible that upregulation or increased efficacy of this enzymatic pathway could evolve. Aromatase activity occurs in mammary tissue [13] and could allow the development of male mammary glands

to proceed through initial stages of feminisation – the proliferation of ectodermal tissue into a mammary bud, duct formation and, at puberty, proliferation of glandular and stromal tissue.

At first glance, the pregnancy/lactation stage of mammary development appears impossible for males. However, it is the hormonal changes that occur during pregnancy rather than the presence of a developing foetus that appear to provide the necessary stimuli for final glandular growth and milk letdown. Prolactin-dependent mammogenesis can begin before placental establishment in pregnant or pseudopregnant rodents [14]. Even in the absence of a preceding pregnancy, lactation can be induced by the administration of exogenous hormones and/or suckling stimulation [15,16]. Moreover, placental hormones are not important for full lactation in all mammals. For example, non-pregnant female dwarf mongoose *Helogale parvula*, and domestic dogs, *Canis lupus familiaris*, are hormonally primed for lactation by pseudopregnancy [15,17] and, even without pseudopregnancy, lactation has been observed in goats, *Capra hircus* [18], laboratory rats, *Rattus norvegicus*, captive primates and even humans [15]. Lactation following parturition is induced by a surge in prolactin, although the precise mechanism varies. In some species, high concentrations of estrogens inhibit the action of prolactin, and a sharp drop in postpartum estrogen and progesterone levels removes this inhibition, allowing prolactin to surge and act upon mammary glands [19]. High levels of estrogen produce the same effect in other species [20]. These observations suggest that a rapid change in the ratio of estrogen to progesterone is a key factor for disinhibition of pituitary prolactin release [9]. Prolactin is found in male as well as female mammals, and prolactin surges in males, comparable to those of females in late pregnancy, can occur spontaneously [9]. Additionally, plasma prolactin levels can increase in males in response to manual nipple stimulation [21]. Thus, if the initial priming of mammary glands had occurred, prolactin surges could induce male lactation.

One potential avenue for the advent of male lactation might lie in the homology that exists between growth hormone and prolactin. Although variation exists across species, up to 25% of the primary amino acids of these hormones are identical [22], which suggests they have a common precursor [19,20]. Growth hormone and the structurally similar placental lactogen have been considered lactogenic because of their ability to promote lobulalveolar growth and milk secretion in various bioassays in some strains of laboratory mice [19,23]. Thus, because prolactin – the critical determinant and/or maintainer of mammary glands and lactation – and growth hormone are structurally similar and because conversion of testosterone to estrogen is possible, insurmountable physiological constraints on male lactation are unlikely.

That males can, in principle, lactate is supported by a wealth of data. For example, lactation in men was observed in World War II prisoner of war camps when malnourished detainees were later liberated and provided with adequate nutrition [24]. During the period of limited food supply, the prisoners suffered liver, testicular and pituitary atrophy. After postrelease increases in nourishment, the testes and

pituitary gland rapidly regained their function and began producing estrogens and androgens. However, the liver was slower to recover from the stress of starvation and could not metabolise these products [24]. The result was an imbalance of hormones that led to male lactation. Liver cirrhosis caused by alcoholism or other stresses to the liver can cause a similar condition [24], and because the hypothalamus normally inhibits the release of prolactin from the pituitary gland [20], pituitary tumours, other pathology or malnutrition can prevent proper functioning of this axis which can then release prolactin and also lead to male lactation [24].

Lactation outside of pregnancy is not always associated with a pathological state or malnutrition. Lactation in virgin and non-pregnant female sheep, *Ovis aries*, as well as in some males, has been observed without signs of tumours or poor nutrition [25–27]. These cases were eventually linked to estrogen-like compounds in the plants upon which they were feeding. It is now known that more than 50 plant species contain estrogen mimics known as phytoestrogens [28,29]. Although the mechanisms are not completely understood, several plant secondary metabolites, mostly from the flavonoid family, can mimic the effects of steroidal estrogens. These non-steroidal compounds have similar overall structures or active sites as natural steroidal estrogen and can compete for binding sites on estrogen receptor proteins [29,30]. Thus, plant compounds can have effects similar to endogenous estrogens [30,31].

Other exogenous compounds that mimic estrogen structure and function and affect reproduction include breakdown products of organic pesticides [31]. For example, when fed to rats, the commonly used herbicide altrazine induced changes in mammary structure consistent with persistent estrogen and prolactin exposure [28]. Similarly, the decrease in human sperm counts has been attributed to the alteration of gonadotropins via the effects of environmental estrogens on the hypothalamic/pituitary axis [31]. Anti-androgens, like environmental estrogens, are also common [31]. For example, exposure to vinclozolin, a commonly used fungicide and anti-androgen, stimulated nipple development in male rats [30]. Given that males can lactate, why do we not see more evidence of male lactation in mammals?

Selection and male lactation

Lactation allows females to feed offspring from maternal energy reserves, somewhat independently of fluctuations in food supply. This conclusion is supported by models showing that even when lactation is very costly and inefficient in terms of energy lost during processing, it can still provide substantial fitness advantages in the face of an unreliable food supply [32]. One evolutionary argument often invoked to explain the general lack of male lactation has been that female reproductive success is not limited by the ability of a female to lactate [33]. That is, there is never any selection for male lactation because fitness is maximised with female lactation alone. However, this does not appear to be a sustainable argument (Box 2). So what could select for male lactation?

From the evidence presented above, certainty of paternity is one factor that could influence selection on male

lactation, and thus male lactation could potentially evolve in situations of strict genetic monogamy. Related to this is the issue of alternative mating opportunities [2,8]. If males had no chance of securing matings with additional partners, then selection to withhold care and reallocate the saved resources to new matings would be minimal. Additionally, if care from two parents is needed for the survival of offspring, a male might do better to ensure the survival of current progeny rather than search for additional matings [7,34]. These and other conditions (or at least some of them) (Box 1) probably must be met to ensure substantial male care, but in addition to this, male lactation itself has to be advantageous. Because male lactation involves some feminisation of males, feminisation should not be costly for male lactation to be favoured by selection. Hence, reduced selection on male-specific functions might additionally be required. In agreement with this argument, lack of male lactation, even in mammals with male care, has been explained by strong male–male competition or males specialising in territory or other resource defence, including defending against predators [8]. Thus, minimal male–male competition and little predation could facilitate the evolution of male lactation. Another factor that could potentially influence selection on male lactation is within-group relatedness [35]. This follows from Hamilton's [36] general rule for the evolution of altruistic behaviour: inclusive fitness benefits could balance costs of milk provisioning and favour male lactation.

Overall, it appears that species with strict monogamy, little pre-copulatory male–male competition, and/or obligate biparental care, and perhaps extreme food unreliability, high male relatedness within groups (and hence high relatedness to all groups' offspring) and low predation, offer the potential for the evolution of male lactation.

Box 2. Is female fitness unconstrained by lactational capacity?

It has been suggested that female reproductive success is not limited by a female's ability to lactate. If this were the case, male lactation would not increase the fitness of a mated pair [33]. Canids, for example, often form monogamous pairs; the female nurses the young and both parents hunt for food to feed the pups. The size of the litter and its survival are independent of the quantity of milk that a female can produce. Instead, the ability of parents to provide food from their territory is the main determinate of pup survivorship [33]. However, this argument potentially confounds cause and effect. It is possible that litter size has been optimised to match female milk output and, if males did lactate, larger litters could be produced and fitness would increase. Additionally, it seems clear that for many female mammals, reduced duration of lactation would allow a new reproductive cycle to begin sooner, and all else being equal, faster rates of reproduction mean higher fitness. Moreover, many rodents, marsupials and some bats exhibit a postpartum estrus [50,51], and if a female becomes pregnant while nursing, there might be an embryonic diapause or delayed implantation of new blastocysts [52]. This delay is variable and the latency is strongly correlated with litter size. The existence of this delay implies that lactational capacity can limit female reproductive potential [9]. In other words, if a female did not need to lactate, pregnancy would proceed uninhibited, the next litter would arrive sooner and the female would be able to enter estrus once again. Thus, arguments based solely on the ability of females to meet lactational demands do not seem to be sufficient to explain a lack of male lactation.

Therefore, assessing these variables seems an obvious place to start when investigating putative adaptive male lactation, although other factors such as variation in male quality could also be important [7].

Old World fruit bats: evidence for adaptive male lactation?

Although much of the evidence presented in this review suggests that male lactation has the potential to evolve, most empirical evidence for male lactation is restricted to domesticated animals or humans under the influence of phytoestrogens, exogenous hormones or pathological states. However, male lactation has been documented in populations of free-ranging Dayak fruit bats *Dyacopterus spadecius* in Malaysia (Figure 1) and the masked flying fox *Pteropus capistrastus* in Papua New Guinea [37,38]. Histological analysis of the Dayak fruit bat revealed well-developed lacteriforus ducts and underlying mammary tissue similar to that found in lactating females [37]. As the biology of the two bat species is largely unknown, it is currently unclear why male lactation occurs in these taxa. Additionally, it is unclear whether male lactation also occurs in other populations of Dayak fruit bat. Is male lactation adaptive or evidence of some underlying health problems?

Figure 1. Lactating male Dayak fruit bat, *Dyacopterus spadecius*, one of the two mega-bat species in which male lactation in the wild has been reported (image courtesy of C.A. Francis).

If stress or some pathology induced male lactation in these species (as seen above), lactation should only be observed in unhealthy males. As part of the first step in understanding male lactation, lactating males could therefore be examined for evidence of poor health. Given the relatively large numbers of male Dayak fruit bats from which milk was expressed [37], it seems unlikely that pituitary tumours are the cause of male lactation – even though these cause lactation in other mammals. Moreover, available evidence suggests that bouts of malnutrition were not the cause of lactation in these male bats. Malnourished males would show little or no active spermatogenesis. However, the testes in the lactating males that were examined histologically showed evidence of active spermatogenesis, with seminiferous tubules showing all stages of developing gametes [37]. Nevertheless, to be confident that males did not lactate because of some pathological condition, examination for evidence of pituitary malfunction or pathology, liver damage or malnutrition should be undertaken.

Although the diets of *D. spadecius* and *P. capistrastus* have not been described in detail, both species feed on fruits and other plant parts, including leaves [38,39]. If leaves that contain phytoestrogens are consumed, it is possible that these compounds might be the initial causative agents of male lactation. Thus, a thorough examination of diet is needed, all the more so because food unreliability is important in selecting for lactation [36]. These species might also be exposed to organochloride pesticides which could potentially induce mammary development via breakdown products. Use of these and other pesticides has increased considerably in recent decades in both in Malaysia and Papua New Guinea [40].

If exogenous influences and pathology can be ruled out as causes of male lactation in these mammals, the possibility exists that male lactation is a unique adaptive phenomenon in these two species. However, because the nipples of lactating male bats were smaller and less cornified than lactating female Dayak fruit bats that had suckled young, males might not be feeding pups [37]. Alternatively, because males express less milk than females – 5 μl versus 350 μl expressed from females [37] – it is possible that some suckling occurs, but not enough to cause enlargement and cornification of the nipples. Moreover, because bats are calcium limited [41–43], the small volume of milk produced by males could be beneficial for offspring. This is particularly likely because bats have longer lactation periods than other mammals of their size [44]. If males are providing milk to their young, then, like females, they should display seasonal cyclicity in mammary gland development, and there is indeed some evidence for this [37].

Much of the preceding discussion is conjecture and, therefore, before benefits to male lactation are invoked, evidence of male nursing must be documented. If it is found to occur, a detailed study of the genetic mating system of these bats and their social structure, plus food distribution and consumption, will be required, and although the mating systems of these bats are currently unknown, obligate (social) monogamy has been reported for only one species of Old World fruit bats, *Pteropus samoensis* [45]. However,

even if males do not suckle their young, this need not rule out evolutionary explanations for male lactation. Perhaps lactating males are signalling their genetic quality as *females* to potential mates ([46] and see Ref. [47]). This is an intriguing, but neglected, possibility.

Conclusion

While many questions remain unanswered, detailed investigation of the factors that could influence the evolution of male lactation is required. This would enable predictions to be made about which taxa are likely to exhibit this character, and under what conditions. Paternal care more generally has been the subject of much theoretical investigation, and this has provided fundamental insight into how and when care should evolve [2,7]. A focussed investigation of male lactation would be similarly enlightening. It is possible that male Dayak fruit bats and masked flying foxes have evolved the ability to produce milk. Obviously, before selective explanations are invoked, proximate explanations such as ingestion of phytoestrogens need to be ruled out, but if males actually are lactating and nursing, these two species provide unique opportunities to independently evaluate the various selective agents thought to be important in the evolution of paternal care. Additionally, research on these species will aid understanding of lactation, and dysfunctional aspects of lactation, in other male mammals, including humans. As Maynard Smith [3] remarked, 'it is odd that no case of male lactation has evolved.' Well, perhaps it has, possibly twice. Additional research is needed to assess this intriguing possibility.

References

1 Speakman, J.R. (2008) The physiological costs of reproduction in small mammals. *Phil. Trans. R. Soc. Lond. B Biol. Sci.* 363, 375–398
2 Kokko, H. and Jennions, M.D. (2008) Parental investment, sexual selection and sex ratios. *J. Evol. Biol.* 21, 919–948
3 Maynard Smith, J. (1978) *The Evolution of Sex.* Cambridge University Press
4 Trivers, R.L. (1972) Parental investment and sexual selection. In *Sexual Selection and the Descent of Man 1871–1971* (Campbell, B., ed.), pp. 136–179, Aldine Publishing
5 Wedell, N. *et al.* (2006) Sexual conflict and life history. *Anim. Behav.* 71, 999–1011
6 Hosken, D.J. and Stockley, P. (2003) Polyandry: a life history perspective. *Evol. Biol.* 33, 173–194
7 Houston, A.I. and McNamara, J.M. (2002) A self-consistent approach to paternity and parental investment. *Philos. Trans. R. Soc. Lond. B Biol. Sci.* 357, 351–362
8 Kokko, H. and Jennions, M. (2003) It takes two to tango. *Trends Ecol. Evol.* 18, 103–104
9 Daly, M. (1979) Why don't male mammals lactate? *J. Theor. Biol.* 78, 325–345
10 Nelson, R.J. (2005) *An Introduction to Behavioral Endocrinology.* Sinauer
11 Wilmer, P. *et al.* (2006) *Environmental Physiology of Animals.* Blackwell Publishing
12 Pfaff, D.W. *et al.* (2004) *Principles of Hormone/Behaviour Relations.* Elsevier
13 Foster, P.A. (2008) Steroid metabolism in breast cancer. *Minerva Endocrinol.* 33, 27–37
14 Knight, C.H. (1984) Mammary growth and development: strategies of animals and investigators. *Symp. Zool. Soc. Lond.* 51, 147–170
15 Creel, S.R. *et al.* (1991) Spontaneous lactation is an adaptive result of pseudopregnancy. *Nature* 351, 660–662
16 Brennan, A.J. *et al.* (2008) A population of mammary epithelial cells do not require hormones or growth factors to survive. *J. Endocrinol.* 196, 483–496
17 Marshall, F.H.A. (1922) *The Physiology of Reproduction.* Longmass, Green and Company
18 Nair, B.R.K. *et al.* (1981) A report on lactating male goats. *Kerala J. Vet. Sci.* 12, 145–150
19 Friesen, H.G. and Cowden, E.A. (1989) Lactation and galactorrhea. In *Endocrinology* (Vol. 3, 2nd edn) (DeGroot, L., ed.), pp. 2074–2086, W.B. Saunders
20 Griffin, J.E. and Ojeda, S.R. (1996) *Textbook of Endocrine Physiology.* (3rd edn), Oxford University Press
21 Kolodny, R.C. *et al.* (1972) Mammary stimulation causes prolactin secretion in non-lactating women. *Nature* 238, 284–286
22 Bennett, G.W. and Whitehead, S.A. (1983) *Mammalian Neuroendocrinology.* Oxford University Press
23 Forsyth, I.A. and Hayden, T.J. (1977) Comparative endocrinology of mammary growth and lactation. *Symp. Zool. Soc. Lond.* 41, 135–163
24 Greenblatt, R.B. (1972) Inappropriate lactation in men and women. *Med. Aspects Hum. Sex.* 6, 25–33
25 Bennetts, H.W. (1946) Metaplasia in the sex organs of castrated male sheep maintained on early subterranean clover pastures. *Aust. Vet. J.* 22, 70–78
26 Moule, G.R. *et al.* (1963) The significance of estrogens in pasture plants in relation to animal production. *Anim. Breed. Abstr.* 31, 139–157
27 Adams, N.R. (1995) Detection of the effects of phytoestrogens on sheep and cattle. *J. Anim. Sci.* 73, 1509–1515
28 Chapin, R.E. *et al.* (1996) Endocrine modulation of reproduction. *Fundam. Appl. Toxicol.* 29, 1–17
29 Usui, T. (2006) Pharmaceutical prospects of phytoestrogens. *Endocr. J.* 53, 7–20
30 Choi, S.Y. *et al.* (2008) Estrogenic activities of isoflavins and flavones and their structure-activity relationships. *Planta Med.* 74, 25–35
31 Panzica, G.C. *et al.* (2007) Effects of xenoestrogens on the differentiation of behaviourally-relevant neural circuits. *Front. Neuroendocrinol.* 28, 179–200
32 Dall, S.R.X. and Boyd, I.L. (2004) Evolution of mammals: lactation helps mothers cope with unreliable food supplies. *Proc. R. Soc. Lond. B Biol. Sci.* 271, 2049–2057
33 Daly, M. and Wilson, M. (1983) *Sex Evolution and Behavior.* Willard Grant Press
34 Magrath, M.J.L. and Komdeur, J. (2003) Is male care compromised by additional mating opportunity? *Trends Ecol. Evol.* 18, 424–430
35 Roulin, A. (2002) Why do lactating females nurse alien offspring? A review of hypotheses and empirical evidence. *Anim. Behav.* 63, 201–208
36 Hamilton, W.D. (1964) The genetical theory of social behaviour. *I. J. Theor. Biol.* 7, 1–16
37 Francis, C.M. *et al.* (1994) Lactation in male fruit bats. *Nature* 367, 691–692
38 Bonaccorso, F.J. (1998) *Bats of Papua New Guinea.* Conservation International
39 Payne, J. and Francis, C.M. (1998) *A Field Guide to the Mammals of Borneo.* The Sabah Society
40 Barfield, S. (1986) International viewpoint: pesticide use in the Third World. *J. Environ. Health* 48, 228–229
41 Barclay, R.M.R. (1994) Constraints on reproduction by flying vertebrates: energy and calcium. *Am. Nat.* 144, 1021–1031
42 Booher, C.M. (2008) Effects of calcium availability on reproductive output of big brown bats. *J. Zool. (Lond.)* 274, 38–43
43 Voigt, C.C. *et al.* (2008) Nutrition or detoxification: why bats visit mineral licks of the Amazonian rainforest. *PloS ONE* 3, e2011
44 Hayssen, V. (1993) Empirical and theoretical constraints on the evolution of lactation. *J. Dairy Sci.* 76, 3213–3233

45 Cox, P.A. (1983) Observations on the natural history of Samoan bats. *Mammalia* 47, 519–523

46 Seger, J. and Trivers, R.L. (1986) Asymmetry in the evolution of female mating preferences. *Nature* 319, 771–773

47 Kvarnemo, C. (2006) Evolution and the maintenance of male care: is increased paternity a neglected benefit of care? *Behav. Evol.* 17, 144–148

48 Queller, D.C. (1997) Why do females care more than males? *Proc. R. Soc. Lond. B Biol. Sci.* 264, 1555–1557

49 Fisher, R.A. (1930) *The Genetical Theory of Natural Selection.* Claredon Press

50 del Barco-Trillo, J. and Ferkin, M.H. (2007) Female meadow voles, *Microtus pennsylvanicus*, experience a reduction in copulatory behaviour during postpartum estrus. *Ethology* 113, 466–473

51 Badwaik, N. and Rasweiler, J.J., IV (2000) Pregnancy. In *Reproductive Biology of Bats* (Crichton, E.D. and Krutzsch, P.H., eds), pp. 222–293, Academic Press

52 Renfree, M.B. and Calaby, J.H. (1981) Background to delayed implantation and embryonic diapause. In *Embryonic Diapause in Mammals* (Flint, A.P.F. *et al.*, eds), pp. 1–9, Cambridge University Press