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Review

Hormonal regulation of offspring begging and mediation of parent–offspring conflict

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Recently, there has been much interest in the role of endogenous and maternal hormones as regulators of offspring begging and mediators of parent–offspring conflict. Here, we review recent work in this field, and identify inconsistencies in the literature. We find good evidence that hormones play a role as regulators of begging: 13 studies report a positive effect on begging and six a negative effect. There is also good evidence that hormones influence offspring fitness, but the direction of reported effects is inconsistent: eight studies report a positive effect on offspring fitness and 10 a negative effect. We explore potential pathways linking hormonal effects on begging and growth. We find that our current understanding of these pathways is incomplete, and suggest a simple model linking hormonal effects on begging and growth. We next discuss the role of hormones as mediators of parent–offspring conflict. We find little evidence that maternal hormones provide a mechanism for parental favouritism. We use graphical models to explore the hypothesis that maternal hormones act as honest signals, and find that costs of hormone production can ensure the honesty of maternal hormones but only under very restricted conditions. We discuss evidence from recent cross-fostering experiments suggesting that maternal hormones act in the context of overlapping interests between parents and offspring. Finally, we highlight the need for more studies on nonavian taxa to establish whether hormonal regulation of begging is specific to birds or general across taxa where offspring beg for food from their parents.

Offspring of many birds and mammals, as well as some insects, solicit food from their parents by engaging in conspicuous begging displays (Kilner & Johnstone 1997). Traditionally, behavioural ecologists have studied begging to gain insight into the outcome of parent–offspring conflict over parental investment (Trivers 1974). Theoretical and empirical research by behavioural ecologists suggests that costly begging is a key mechanism underlying the resolution of parent–offspring conflict because it allows parents to obtain honest and reliable information on offspring needs (Godfray 1995; Kilner & Johnstone 1997; Smiseth et al. 2008). Begging has recently attracted growing attention from behavioural endocrinologists seeking to understand how hormones produced by offspring themselves (hereafter termed endogenous hormones) and hormones deposited into eggs by female parents (hereafter termed maternal hormones) affect begging and parent–offspring conflict (Schwabl & Lipar 2002; Müller et al. 2007a). The aim of this review is to provide an overview of the published work in this field, highlight inconsistencies and deficiencies in the literature, and discuss how these might be addressed in the future. We focus on the following five main issues: (1) evidence that endogenous and maternal hormones act as regulators of begging; (2) evidence that these hormones affect offspring growth and survival; (3) hypotheses for the link between hormonal effects on begging and growth; (4) hypotheses for the role of hormones as mediators of parent–offspring conflict; and (5) the taxonomic bias in the literature towards birds.

HORMONAL REGULATION OF BEGGING

Schwabl (1996) provided the first evidence that hormones play a role in regulating begging. Schwabl manipulated levels of maternally derived testosterone (T), a gonadal sex steroid regulating the development of reproductive tissues and muscles (Adkins-Regan 2005), by injecting T into the yolk of canary, *Serinus canaria*, eggs. He found that nestlings hatching from testosterone-treated eggs spent more time begging than those hatching from control eggs. A few years later, Kitaysky et al. (2001) demonstrated

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a role of endogenous corticosterone (CORT), an adrenal steroid regulating stress responses and immune function (Adkins-Regan 2005), by administering subcutaneous CORT implants to black-legged kittiwake, *Rissa tridactyla*, nestlings. This study found that CORT-implanted nestlings increased their begging frequency compared to control nestlings. We have identified an additional 19 studies that provide information on the effects of hormones on begging (Table 1) by searching Web of Knowledge using the search

Table 1
Summary of evidence for hormonal regulation of begging

Hormone	Origin	Species	Effect	Design	Begging variable	Source
T	Maternal	Canary, *Serinus canaria*	0	Exp	Rate	Schwabl 1996
T	Maternal	Canary	0	Exp	Duration	Schwabl 1996
T	Maternal	Canary	+	Exp	Time	Schwabl 1996
T	Maternal	Canary	0	Exp	Proportion*	Müller et al. 2010
T	Maternal	Canary	0	Exp	Duration*	Müller et al. 2010
T	Maternal	Canary	0	Exp	Rate*	Müller et al. 2010
T	Maternal	Canary	0	Exp	Posture†	Müller et al. 2010
T	Maternal	Black-headed gull, *Chroicocephalus ridibundus*	0	Exp	Call rate‡	Eising & Groothuis 2003
T	Maternal	Black-headed gull	+	Exp	Reaction	Eising & Groothuis 2003
T	Maternal	Black-headed gull	0	Exp	Approach	Eising & Groothuis 2003
T	Maternal	Black-headed gull	0	Exp	Pump latency§	Eising & Groothuis 2003
T	Maternal	Black-headed gull	0	Exp	Peck latency	Eising & Groothuis 2003
T	Maternal	Black-headed gull	+	Exp	Pump rate§	Eising & Groothuis 2003
T	Maternal	Black-headed gull	0	Exp	Peck rate	Eising & Groothuis 2003
T	Maternal	European starling, *Sturnus vulgaris*	0	Exp**	Frequency††	Pilz et al. 2004
T	Maternal	European starling	–	Exp**	Latency††, ‡‡	Pilz et al. 2004
T	Maternal	European starling	0	Exp**	Posture††	Pilz et al. 2004
T	Maternal	European starling	–	Exp**	Duration††	Pilz et al. 2004
T	Maternal	European starling	0	Exp**	Frequency§§	Pilz et al. 2004
T	Maternal	European starling	0	Exp**	Latency§§	Pilz et al. 2004
T	Maternal	European starling	0	Exp**	Posture§§	Pilz et al. 2004
T	Maternal	European starling	0	Exp**	Duration§§	Pilz et al. 2004
T	Maternal	Barn swallow, *Hirundo rustica*	0	Exp	Rate***	Saino et al. 2006
T	Maternal	Zebra finch, *Taeniopygia guttata*	0/+†††	Exp	Duration	von Engelhardt et al. 2006
T	Maternal	Yellow-legged gull, *Larus michahellis*	+	Exp	Prehatch‡‡‡	Boncoraglio et al. 2006
T	Maternal	Yellow-legged gull	0	Exp	Rate	Boncoraglio et al. 2006
T	Endogenous	Black-headed gull	–	Exp	Rate	Groothuis & Ros 2005
T	Endogenous	Slender-billed prion, *Pachyptila belcheri*	+	Obs	Call rate	Quillfeldt et al. 2006
T	Endogenous	Pied flycatcher, *Ficedula hypoleuca*	+	Obs	Duration	Goodship & Buchanan 2006
T	Endogenous	Pied flycatcher	+	Obs	Height	Goodship & Buchanan 2006
T	Endogenous	Pied flycatcher	+	Exp	Duration	Goodship & Buchanan 2007
T	Endogenous	Pied flycatcher	+	Exp	Height	Goodship & Buchanan 2007
T	Endogenous	Pied flycatcher	+	Obs	Posture	Buchanan et al. 2007
DHT	Endogenous	Black-headed gull	–	Exp	Rate	Groothuis & Ros 2005
E	Endogenous	Black-headed gull	0	Exp	Rate	Groothuis & Ros 2005
CORT	Maternal	Yellow-legged gull	–	Exp	Prehatch	Rubolini et al. 2005
CORT	Maternal	Yellow-legged gull	–	Exp	Rate	Rubolini et al. 2005
CORT	Endogenous	Black-legged kittiwake, *Rissa tridactyla*	+	Exp	Rate	Kitaysky et al. 2001
CORT	Endogenous	Black-legged kittiwake	+	Exp	Time	Kitaysky et al. 2003
CORT	Endogenous	Slender-billed prion	0	Obs	Call rate	Quillfeldt et al. 2006
CORT	Endogenous	Blue-footed booby, *Sula nebouxii*	0	Exp	Time	Vallarino et al. 2006
CORT	Endogenous	House sparrow, *Passer domesticus*	+	Exp	Rate	Loiseau et al. 2008a
CORT	Endogenous	House sparrow	0	Exp	Posture	Loiseau et al. 2008a
CORT	Endogenous	House sparrow	–§§§	Exp	Mouth colour	Loiseau et al. 2008b
CORT	Endogenous	White-crowned sparrow, *Zonotrichia leucophrys*	–	Exp	Latency‡‡	Wada & Breuner 2008
CORT	Endogenous	White-crowned sparrow	0	Exp	Duration	Wada & Breuner 2008
CORT	Endogenous	White-crowned sparrow	0	Exp	Call rate	Wada & Breuner 2008
Leptin	Endogenous	Slender-billed prion	+	Obs	Call rate	Quillfeldt et al. 2009
Leptin	Endogenous	Slender-billed prion	0	Obs	Duration	Quillfeldt et al. 2009
JH	Endogenous	*Nicrophorus vespilloides*	+	Exp****	Time	Crook et al. 2008

Column 1 refers to hormone of interest (T = testosterone, DHT = dihydrotestosterone, E = oestradiol, CORT = corticosterone, JH = juvenile hormone), column 2 indicates whether the hormone is deposited into the egg yolk by the female parent or produced endogenously by the offspring, column 4 lists reported effects on begging (+ = increases begging, – = decreases begging, 0 = no effect), column 5 indicates whether hormone levels were manipulated experimentally (exp) or not (obs), and column 6 indicates the begging parameters that were recorded.

* Effect on begging measured 1 h after hatching.
† Effect on begging measured 8–10 days after hatching.
‡ Number of calls per begging bout.
§ Pump: up and down head movements, accompanied by a call during the downward movement.
** T treatment 10 times higher than natural level of T for species (Groothuis et al. 2005a).
†† Begging in response to acoustic stimuli.
‡‡ Treatment decreased begging by increasing begging latency.
§§ Begging in response to vibrational stimuli.
*** Effect on begging measured 10 days after hatching.
††† Treatment had a sex-specific effect on nestling begging, increasing begging in female but not in male nestlings.
‡‡‡ Effect on loudness of embryonic vocalizations.
§§§ Treatment had condition-dependent effect; CORT-treated nestlings had less colourful mouth flanges only when in poor condition.
**** Unclear whether treatment is within natural variation of JH for species.