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Empirical evidence for multiple costs of begging in poison frog tadpoles

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ABSTRACT

In recent decades, theoretical and empirical work has investigated the relative roles of costs and benefits in inhibiting excessive displays of begging to parents. Whether costs are important in maintaining reliability of offspring signals is still debated, in part because empirical evidence for costs is conflicting. Nearly 90% of empirical studies have focused on birds. Costs may differ between birds and other animal groups, but more information is needed about non-avian systems. In this study, we tested for evidence of costs of begging in an anuran, *Oophaga pumilio*, in which tadpoles vibrate vigorously against mother frogs to solicit nutritive eggs. First, we tested whether a realistic manipulation of begging effort affected tadpole growth over two weeks, and found evidence for such physiological costs. Second, we tested whether the presence of a natural predator would alter begging behavior. Tadpoles begged when hungry, but begged significantly less when both hungry and viewing a spider, suggesting that they have evolved to reduce potential costs of predation risk when begging. Thus, we demonstrate the first example of costs via both physiological expenditure and predation risk in a non-avian species. Unlike most birds which rear offspring in clutches, *O. pumilio* mothers rear tadpoles in individual sites, suggesting that in the absence of sibling effects, multiple costs of begging work concomitantly to prevent the expression and evolution of excessive or indiscriminate signaling. Future studies of begging from a comparative perspective will continue to augment our understanding of the mechanisms behind the evolution of parent-offspring communication.

1. Introduction

Offspring in many taxa exhibit begging behavior prior to receiving care from parents. Elucidating the interaction between begging and the allocation of parental resources is key to understanding the apparent evolutionary conflict of interest among parents and their offspring with regards to the intensity and duration of parental care (reviewed in Mock et al., 2011, Redondo et al., 2016). Many studies in recent decades have attempted to identify the reasons why offspring would limit their degree of begging display rather than escalate their effort indiscriminately to solicit additional care from parents (reviewed in Martín-Gálvez et al., 2011; Mock et al., 2011; Redondo et al., 2016). It is thought that excessive begging is kept in check by the balance between the relative costs and benefits of begging and receiving care.

However, evidence of costs is inconsistent, and whether costs are necessary or sufficient to prevent exaggeration to parents remains an issue of contention (see Moreno-Rueda, 2007; Redondo et al., 2016). A series of theoretical models have debated the relative importance of costs and benefits, proposing varied scenarios in which the reliability of begging signals might be evolutionarily maintained if costs are present, minimal, or even absent (reviewed in Mock et al., 2011; Akçay, 2012; Redondo et al., 2016). Potential costs of begging fall into two general categories: (1) predation risk or (2) physiological expenditure (energetic, metabolic, oxidative, immune, growth, or metabolic costs; Table 1). But, abundant empirical studies that evaluate those costs provide conflicting results (see Table 1).

Early studies supported the hypothesis that begging increases predation risk, at least under certain criteria of nest location and clutch size (Redondo and Castro, 1992; Haskell, 1994; Leech and Leonard, 1997). Later studies varied, either finding or not find-

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Table 1
List of empirical studies of the costs of begging behavior, organized by type of cost and taxonomic group.

Authors	Year	Group	Taxon	Type of Cost	Evidence for Costs?
Weary et al.	1996	Mammals	Domestic pig	Crushing	Yes
Schleich & Busch	2004	Mammals	Tuco-tuco	Energetic	No
Bell	2007	Mammals	Banded mongoose	Growth	Yes
Smiseth & Parker	2008	Insects	Burying beetle	Growth	No
Mäenpää et al.	2015	Insects	Burying beetle	Not indicated	Yes
Andrews & Smiseth	2013	Insects	Burying beetle	Survival	Yes
Yoshioka et al.	2016	Frogs	Mimic poison frog	Development	Some
Yoshioka et al.	2016	Frogs	Mimic poison frog	Growth	Some
Nettle et al.	2017	Birds	European starling	DNA damage	Yes
Moreno-Rueda et al.	2016	Birds	Pied flycatcher	Ectoparasite	Yes
Buchanan et al.	2007	Birds	Canary	Energetic	Yes
Glassey et al.	2014	Birds	Common grackle	Energetic	Low
Soler et al.	1999	Birds	Cuckoo	Energetic	Low
Neuenschwander et al.	2003	Birds	Great tit	Energetic	Yes
Soler et al.	2014	Birds	House sparrow	Energetic	Yes
Chappell & Bachman	1998	Birds	House wren	Energetic	Low
Bachman & Chappell	1998	Birds	House wren	Energetic	Low
Soler et al.	1999	Birds	Magpie	Energetic	Low
Martín-Gálvez et al.	2011	Birds	Magpie	Energetic	No
Moreno-Rueda & Redondo	2011	Birds	Southern shrike	Energetic	Yes
Leech & Leonard	1996	Birds	Tree swallow	Energetic	Low
McCarty	1996	Birds	Various	Energetic	Low
Jurisevic et al.	2015	Birds	Various	Energetic	Yes
Abraham & Evans	1999	Birds	White pelican	Energetic	Yes
Weathers et al.	1997	Birds	Zebra finch	Energetic	Low
Kilner	2001	Birds	Canary	Growth	Yes
Nettle et al.	2017	Birds	European starling	Growth	Yes
Maronde & Richner	2015	Birds	Great tit	Growth	No
Kedar et al.	2000	Birds	House sparrow	Growth	No
Loiseau et al.	2008	Birds	House sparrow	Growth	Yes
Morena-Rueda	2010	Birds	House sparrow	Growth	No
Soler et al.	2014	Birds	House sparrow	Growth	Yes
Rodríguez-Gironés et al.	2001	Birds	Magpie	Growth	Yes
Moreno-Rueda et al.	2012	Birds	Magpie	Growth	Yes
Halupka	1998	Birds	Meadow pipit	Growth	Yes
Redondo et al.	2016	Birds	Pied flycatcher	Growth	No
Rodríguez-Gironés et al.	2001	Birds	Ring dove	Growth	No
Moreno-Rueda & Redondo	2012	Birds	Southern shrike	Growth	No
Leonard et al.	2003	Birds	Tree swallow	Growth	No
Royle et al.	2006	Birds	Zebra finch	Growth	No
O'Connor et al.	2014	Birds	Darwin's finch	Immune	Yes
Loiseau et al.	2008	Birds	House sparrow	Immune	Yes
Moreno-Rueda	2010	Birds	House sparrow	Immune	Yes
Soler et al.	2014	Birds	House sparrow	Immune	Yes
Moreno-Rueda et al.	2012	Birds	Magpie	Immune	Yes
Redondo et al.	2016	Birds	Pied flycatcher	Immune	Yes
Moreno-Rueda & Redondo	2011	Birds	Southern shrike	Immune	Yes
Moreno-Rueda & Redondo	2012	Birds	Southern shrike	Immune	Yes
Thomas & Shutler	2001	Birds	Tree swallow	Immune	No
Nettle et al.	2017	Birds	European starling	Inflammation	Yes
Zandberg et al.	2014	Birds	Jackdaw	Not indicated	Yes
Boncoraglio et al.	2012	Birds	Barn swallow	Oxidative	No
Helfenstein et al.	2008	Birds	Great tit	Oxidative	Yes
Maronde & Richner	2015	Birds	Great tit	Oxidative	Some
Moreno-Rueda et al.	2012	Birds	Magpie	Oxidative	Yes
Hall et al.	2010	Birds	Red-winged blackbird	Oxidative	No
Noguera et al.	2010	Birds	Yellow-legged gull	Oxidative	Yes
McDonald et al.	2009	Birds	Bell miner	Predation	Yes
Wegrzyn & Leniowski	2015	Birds	Blackcap	Predation	Yes
Haskell	1994	Birds	Bluebird	Predation	Yes
Ibáñez-Álamo et al.	2012	Birds	Common blackbird	Predation	Yes
Dearborn	1999	Birds	Cowbird	Predation	Yes
Anderson et al.	2010	Birds	Grey warbler	Predation	Yes
Serra & Fernández	2011	Birds	House wren	Predation	Yes
Redondo & Castro	1992	Birds	Magpie	Predation	Yes
Halupka	1998	Birds	Meadow pipit	Predation	No
Barati & McDonald	2017	Birds	Noisy miner	Predation	Yes
Briskie et al.	1999	Birds	Passerines	Predation	Yes
Kostoglou et al.	2017	Birds	Red-capped plover	Predation	No
Bernath-Plaisted & Yasukawa	2011	Birds	Red-winged blackbird	Predation	No
Yasukawa	2016	Birds	Red-winged blackbird	Predation	No
Maurer et al.	2003	Birds	Scrubwren	Predation	No
Platzen & Magrath	2004	Birds	Scrubwren	Predation	Low
Magrath et al.	2007	Birds	Scrubwren	Predation	Yes
Haff & Magrath	2010	Birds	Scrubwren	Predation	Yes
Haff & Magrath	2011	Birds	Scrubwren	Predation	Yes

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