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MATING STRATEGIES AND PARENTAL CARE IN GLASSFROGS (AMPHIBIA ANURA CENTROLENIDAE)

ANYELET VALENCIA-AGUILAR

Tese apresentada ao Instituto de Biociências do Câmpus de Rio Claro, Universidade Estadual Paulista, como parte dos requisitos para obtenção do título de doutora em Ciências Biológicas (Área de concentração: Zoologia).

Março-2020

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TÍTULO DA TESE: MATING STRATEGIES AND PARENTAL CARE IN GLASSFROGS (AMPHIBIA ANURA CENTROLENIDAE)

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CONTENTS

ABSTRACT

Many species in the Centrolenidae family, know as glassfrogs, exhibit paternal care of eggs. Although parental care promotes offspring survival, it may impose survival and mating cost; hence, males should intensify or weaken resource allocation between its fitness' components. Furthermore, anuran males compete to attract females, but since it is an energetically demanding activity, in some cases individuals use some tactics to offset these costs and gain access to mates. In this thesis, I studied different aspects of the paternal care and mating strategies in glassfrogs species, which were separated in four chapters. In chapter 1, we made field observations and conducted behavioral experiments in attending and non-attending males of the glassfrog *Hyalinobatrachium cappellei* to examine the importance of attending activities on offspring survival, as well as the effects of predation risk on male's behavior. We also assessed how parental care influences time allocation in males' activities. We found that care activities do not affect male's mating success and that paternal care is crucial to avoid embryo dehydration. Besides, our results show that although attending males are more risk tolerant, they will prioritize their own survival, even with negative effects on offspring, when the threat reaches a certain threshold. In chapter 2, we examined female mate preference in *H. cappellei*. Our results indicate that females of *H. cappellei* do not select males based on body condition, call persistence, or territory characteristics. Instead, females choose males based on care status; attending males had higher chance of attracting new females and gain new clutches. Additionally, we also found that males adjust their parental care effort in response to genetic relatedness, by caring only for their own

offspring; however, they may remain close to unrelated clutches as a strategy to attract females and increase chances of successful mating. In chapter 3, we experimentally investigated the existence of allopaternal care in two centrolenid species, *Hyalinobatrachium chirripoi* and *Centrolene peristicta,* as well as the possible costs and benefits of this behavior. Attending males of both species males adopted unrelated clutches, whereas non-attending males abandoned their territories when unrelated clutches were placed close to them. Contrary to our expectations, once males adopted the unrelated clutches, they cared for all the eggs in their territories with a similar frequency. Our finding suggest that alloparenting in glassfrogs only occurs in males that already have clutches of their own and, most likely, cannot distinguish unrelated clutches. Finally, in chapter 4, we tested whether glassfrog males that care for their offspring have smaller relative testes volume compared with species that do not exhibit paternal care. We collected data on testis size of breeding frogs using information from specimens we have collected, as well as from museum specimens, and literature. For the 26 species of glassfrogs included in our data set, we found that attending males tend to have smaller testes compared with non-attending males in glassfrogs. Besides, no significant effects of clutch size on testes size were detected. These results suggest that testes size may also vary in response to a pots-fertilization investment, such as parental care.

Keywords: Parental care, offspring, female choice, aloparental care, testes size

RESUMO

Em muitas espécies da família Centrolenidae, conhecidas como rãs-de-vidro, os machos cuidam de seus ovos. No entanto, apesar do cuidado paternal aumentar a sobrevivência da prole, pode impor custos de sobrevivência e acasalamento, portanto, os machos devem aumentar ou diminuir a alocação de recursos entre os componentes do seu *fitness*. Além disso, os machos competem para atrair fêmeas, mas, como é uma atividade exigente em termos energéticos, em alguns casos os indivíduos usam algumas táticas alternativas para compensar esses custos e obter acesso às parceiras. Nesta tese, eu estudei diferentes aspectos do cuidado paternal e estratégias de acasalamento nas rãs-de-vidro, separados em quatro capítulos. No capítulo 1, fizemos observações de campo e realizamos experimentos comportamentais com machos e desovas de *Hyalinobatrachium cappellei* para examinar a importância do cuidado na sobrevivência da prole, bem como avaliamos os efeitos do risco de predação no comportamento dos machos. Também avaliamos como o cuidado paternal influencia a alocação de tempo nas atividades dos machos. Descobrimos que as atividades de cuidado não afetam o sucesso de acasalamento nos machos e que o cuidado paterno é crucial para evitar a desidratação dos embriões. Além disso, nossos resultados mostraram que, embora os machos que cuidam desovas sejam mais tolerantes ao risco, eles priorizam sua própria sobrevivência, mesmo com efeitos negativos para a prole, quando a ameaça atinge um certo limiar. No capítulo 2, examinamos a preferência por parceiros nas fêmeas de *H. cappellei*. Nossos resultados indicam que as fêmeas não escolhem machos com base na condição corporal, persistência do canto

ou características do território. Em vez disso, as fêmeas escolhem machos com base no *status* de cuidado; machos com desovas tiveram maior chance de atrair novas fêmeas e ganhar novas desovas. Além disso, os machos ajustam seu esforço de cuidado em resposta ao grau de parentesco genético, cuidando apenas de suas próprias desovas. No entanto, eles podem permanecer próximos de desovas não relacionadas como uma estratégia para atrair fêmeas e aumentar as chances de acasalamento. No capítulo 3, investigamos, experimentalmente, a existência de cuidado aloparental em duas espécies de centrolídeos, *Hyalinobatrachium chirripoi* e *Centrolene peristicta*, bem como os possíveis custos e benefícios desse comportamento. Machos com desovas de ambas as espécies adotaram desovas não relacionadas, enquanto machos sem desovas abandonaram seus territórios quando as desovas não relacionadas foram colocadas em seus territórios. Contrariamente às nossas expectativas, uma vez que os machos adotaram as desovas não relacionadas, eles cuidaram de todos os ovos em seus territórios da mesma forma e constância. Nossos resultados sugerem que o cuidado aloparental nas rãs-de-vidro ocorre apenas em machos que já possuem desovas próprias e, muito provavelmente, não conseguem distinguir as desovas não relacionadas. Finalmente, no capítulo 4, testamos se os machos das espécies de rãs-de-vidro que cuidam das desovas têm volumes testiculares menores em comparação com as espécies que não exibem cuidados paternos. Coletamos dados sobre o tamanho dos testículos de machos reprodutivos a partir de espécimes em coletados em campo, bem como de espécimes de museus e a partir de literatura. Para as 26 espécies de rãs-de-vidro incluídas em nosso estudo, descobrimos que os machos que cuidam da sua prole têm testículos menores em comparação com os machos que não

cuidam. Além disso, não foram detectados efeitos significativos do tamanho da desova no tamanho dos testículos. Esses resultados sugerem que o tamanho dos testículos também pode variar em resposta a um investimento pós-fertilização, como o cuidado paternal.

Palavras-chaves: Cuidado parental, prole, escolha pela fêmea, cuiado aloparental, tamanho testicular

INTRODUCTION

Mating system is shaped by the reproductive strategies of males and females (Arnold and Duvall 1994), affecting their respective potential rates of reproduction (Clutton-Brock and Vincent 1991). For example, by mating with many females, males can typically increase the number of offspring that they produce. Thus, males are limited in their reproductive success by their access and monopolization of receptive females (Trivers 1972, Arnold and Duvall 1994). Usually males compete to attract females, through male-male competition (intrasexual selection) or display traits that signal their quality as mates (intersexual selection) (Trivers 1972, Andersson 1994). In species where males provide benefits that directly affect female's and offspring fitness, such as nest sites, territories and parental care, there should be strong selection on females to choose males that reliably reflect their ability to provide these direct benefits (Zahavi 1975, Price et al. 1993).

Particularly, in species with paternal care, parents provide care for their offspring and try to increase offspring survival exhibiting simple or elaborate forms of care (Trivers 1972, Ridley 1978, Smiseth et al. 2012). Parental care is broadly defined as any investment in offspring following fertilization of the female gamete (Trivers 1972, Smiseth et al. 2012). Trivers (1972) defined parental care in terms of the reproductive investment of the parent. That is, parental investment is any energy spent to increase the quality or future fitness of an offspring, at the cost of future reproductive success of the breeder, either in the form of reduced condition of the parent, or loss of mating opportunity (Trivers 1972). This inequality between the resource demands of the offspring and the

fitness demands of the parent results in conflict (Klug et al. 2012), leading to a considerable variation in the level and duration of care that parents provide to their offspring (Klug et al. 2012). For example, in some taxa, females invest not only in producing eggs or live offspring but also in care, while in others only the males invest in offspring care (Clutton-Brock 1991, Gross 2005). However, in some cases, parental investment can be equally shared and both parents invest substantial energy and time in parental care (Clutton-Brock 1991). Among vertebrate groups, amphibians show elaborate and conspicuous social and reproductive behaviors and many species with parental care have a terrestrial or semi-terrestrial mode of reproduction (McDiarmind 1978, Crump 1996, Lehtinen and Nussbaum 2003, Gomez-Mestre et al. 2012), making them a natural model system to investigate the relationship between parental investment and mating strategies (McDiarmind 1978, Ursprung et al. 2011, Gomez-Mestre et al. 2012, Summers and Tumulty 2014).

Parental care in amphibians is diverse and know in about 62% of anuran species (35 families) (Furness and Capellini 2019). Care behaviors probably evolved as a response to harsh or unpredictable environmental conditions, high levels of predation, parasitism or intense inter or intraspecific competition on land (Clutton-Brock 1991, Crump 1996, Wells 2007). Therefore, males, females or both display a broad set of parental behaviors, from egg attendance to froglet transport and viviparity to increase offspring survival (Furness and Capellini 2019, Vági et al. 2019). Egg attendance by the male is the commonest form of care in anurans (Vági et al. 2019) and is related with egg protection from pathogens and predators, desiccation (maybe the most important), and handling to prevent developmental abnormalities (McDiarmid 1978, Townsend et al.

1984, Crump 1996, Lehtinen and Nussbaum 2003, Wells 2007). Egg attendance is associated to the permanence of the parent with one or multiple clutches after oviposition, usually at male's territories (McDiarmind 1978, Crump 1996, Lehtinen and Nussbaum 2003, Wells 2007). Some authors have argued that paternal care probably evolve in circumstances where females lay eggs directly in a territory defended by a male (Ridley 1978, Townsend 1986, Werren et al. 1980). Indeed, if a male defends a territory before fertilization, then that sex can be selected as caregiver by association with their offspring and territoriality (territoriality hypothesis; Ridley 1978, Gross and Shine 1981). Consequently, if a male remains in his territory, it is possible that further females will lay their eggs there, reducing the care cost for males (Trivers 1972, Crump 1996). This hypothesis has shown to be plausible in males of numerous species of centrolenids (Greer and Wells 1980, Vockenhuber et al. 2008, Delia et al 2010, Valencia-Aguilar et al. 2012, Delia et al. 2017) and dendrobatids (Weygoldt 1987, Roithmair 1994, Summers and Tumulty 2014), which attend multiple clutches in their territories. In such cases, it is possible that males can offset the care costs by increasing their parental fitness (Lehtinen and Nussbaum 2003). For example, although in *Eleutherodactylus coqui* males lose additional mating opportunities, they improve their reproductive success by providing care to their eggs until hatching (Townsend et al. 1984, Townsend 1986). Besides, as territory defense is energetically expensive, male territoriality associated with parental care likely serve as an honest signal of male quality to females (McDiarmid 1978, Nazareth and Machado 2010, Mangold et al. 2015).

Other important aspects regarding paternal care costs may include mode of fertilization and genetic relatedness between male and offspring (Werren et al. 1980,

Klug et al. 2012). As mentioned above, in species with external fertilization and territorial males, females will lay eggs on the male's territory (Ridley 1978, Crump 1996, Lehtinen and Nussbaum 2003). As a consequence, external fertilization in territorial species could favor the evolution of male care (Ridley 1978, Gross and Shine 1981) because the low sperm competition will increase the level of genetic relatedness between male and offspring, and hence the certainty of paternity (paternity hypothesis; Werren et al. 1980, Gross and Shine 1981, Alonzo and Klug 2012). In this sense, it has been pointed out that parents should invest more in the care of an offspring with a higher degree of relatedness (Alonzo and Klug 2012), since paternal care represents a cost for males (Simon 1983, Townsend 1986). Indeed, models and experimental studies in fishes (Neff and Gross 2001, Neff 2003) and amphibians (Werren et al. 1980, Chen et al. 2011, 2013) have evidenced that males adjust their parental effort in response to variation in parentage degree. However, besides the “certainty of paternity”, other factors as environmental conditions (quality and availability of resources), costs-benefits or mating strategies can lead to variation in parental care behavior (Zahavi 1975, Lion and van Baalen 2007, Alonzo and Klug 2012, Chen et al. 2011).

A parental care strategy employed by some groups is named alloparental care (Riedman 1982, Brown 1998, Ramos et al. 2012), which is defined as the parental investment given by a conspecific individual that is not the genetic father (Wisenden 1999). Although, alloparental behavior can be very beneficial by increasing brood fitness and the reproductive output of the breeder (Wisenden 1999), it entails potential costs to the fecundity and fitness of the alloparent. In fact, individuals may lose all future reproductive potential by taking on the role of alloparent (Roldán and Soler 2011).

However, when the indirect reproductive benefits of adoption outweigh the direct fitness costs, care for unrelated offspring can be used as a strategy (Kalmbach 2006). For example, in Tessellated darters (*Etheostoma olmstedi*, Osteichthyes), females prefer males already associated with eggs, thus males can increase their attractiveness and mating success by caring for unrelated offspring (Stiver and Alonzo 2011). Likewise, males can adopt or include unrelated eggs/youngs into their nest to benefit from decreased offspring predation due to dilution effect, as observed in the cichlid *Cichlasoma nigrofasciatum* (Wisenden and Keenleyside 1994). On the other hand, in the absence of reliable cues to paternity (i.e. by clutch piracy or cuckoldry), selection may favor alloparental behavior in males to avoid potential costs of abandoning their own offspring (Trivers 1972, Clutton-Brock 1991).

As time and energy are limited, any investment in current reproduction may preclude investment in future reproduction or other components of fitness (Gadgil and Bossert 1970, Stearns 1992). For instance, if a male expends energy on current matings by means of sexual ornamentation or gonadal expenditure will have less energy available to offspring assistance (Gadgil and Bossert 1970, Stearns 1992, Requena and Alonzo 2017). Theoretical and experimental studies have considered that energetic limitations can become apparent in male sexual traits (Stiver and Alonzo 2009, Beltran et al. 2010). Indeed, specific sexual morphological features are known to be associated with the mating system in several groups (Pircher et al. 2005, Awata et al. 2006, Soulsbury 2010, Liao et al. 2011, Mascaro et al. 2013), in which it has been established a positive correlation between gonadal expenditure and alternative mating tactics, such as polyandry and clutch piracy, because of sperm competition (Byrne et al. 2002, Vieites

et al. 2004, Pircher et al. 2005). Furthermore, in species with paternal care, as larger testes provide an advantage in sexual competition because they can produce more sperm (Pitnick 1996), males may have evolved large testes to secure paternity and ensure that their efforts benefit their own offspring (Pitnick 1996).

In the glassfrogs (Centrolenidae family), all species are nocturnal and females lay clutches on the vegetation or rocks out of water, along lotic systems (streams and waterfalls), and, following hatching, larvae finish development in the water (McDiarmid 1978, Cisneros-Heredia and McDiarmid 2007, Guayasamin et al. 2009). Parental care of eggs is the main form of parental behavior in this family, with males protecting eggs from predators and desiccation (Jacobson 1985, Hawley 2006, Vockenhuber 2009, Delia et al. 2013, Lehtinen et al. 2014). However, maternal egg attendance has recently been described for one species of glassfrog (Bravo and Delia 2015). Parental care in this family has evolved in species of Centroleninae and Hyalinobatrachinae subfamilies (McDiarmid 1978; Wells 2007, Vargas-Salinas et al. 2014), where high reproductive success has been associated with egg and embryo attendance at male's territory (McDiarmind 1978, Vockenhuber et al. 2008, 2009; Delia et al. 2010, 2013, Valencia-Aguliar et al. 2012, Lehtinen et al. 2014, Delia et al. 2017). Here, we used glassfrog species as models to study mating strategies and parental behavior. In Chapter 1, we assessed how parental care influences time allocation in males' activities, tested the importance of attending activities on offspring survival in *Hyalinobatrachium cappellei*, as well as the effects of predation risk on male's behavior. In Chapter 2, using behavioral and molecular data, we tested hypotheses about the fitness consequences of parental care and the drivers of female mate choice in *H. cappellei*. In Chapter 3, we assessed in

the field the existence of allopaternal care in males of *Hyalinobatrachium chirripoi* and *Cenrolene peristicta* and discussed possible costs and benefits. Finally, in Chapter 4, we investigated whether testes size is related with paternal care in glassfrog males.

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GENERAL CONCLUSION

Prevailing knowledge poses that parental care can be time consuming, energetically demanding, expose parents to predation or disease and decrease their mating success. However, recent discussions suggest that the trade-off between current and future mating success might be more complex than previously assumed. In fact, although parental care can decrease mating success in some species (i.e. fishes, birds, and mammals), where caregiver will not accept new mates. We found that in the glassfrog *Hyalinobatrachium cappelli* females prefer males that provide parental care, thus the evolution of paternal care in this family might be favored also by sexual selection. In this case, if care was favored by sexual selection, are costs likely substantially reduced for parents? Although we do not have enough evidence to answer this question our results suggest that care could be in fact energetically less costly than calling. This because, care can also be used as a strategy to increase males' mating success, decreasing males' costs associate to matting effort. Besides, in glassfrog males do not have cost associated with nest building, feeding, or actively defending of their offspring.

Besides, we found that paternal care, as a mating strategy, can increase males´ mating success but also constrains males' gonadal investment driven likely by the inverse relationship between testosterone level and caregiving. Further studies are needed to elucidate other important questions raised in this study, such as the underlying mechanisms driving alloparental care behavior in glassfrogs. Finally, our results highlight the importance of natural history to uncover trends and generate testable hypotheses about mating strategies and behavior evolution in frogs.