



From cannibal to caregiver: tracking the transition in a cichlid fish

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Although the consumption of one's own offspring is often viewed as maladaptive, under some circumstances this behaviour can be a beneficial way to terminate parental care. When the costs of providing care are extremely high or the benefits of performing care are especially low, parents will sometimes cannibalize their own young, which is called filial cannibalism. This behaviour enables them to cease to care while recouping lost energy. Most studies examining the link between the cost/benefit ratio of care and filial cannibalism have focused on species with male-only care. In contrast, filial cannibalism in biparental caring species has been studied only rarely. To increase our understanding of filial cannibalism in biparental species and examine the transition from cannibal to caring parent, we conducted four experiments with *Neolamprologus caudopunctatus*, a biparental cichlid fish from Lake Tanganyika, Africa. First, in experiment 1 we show that the establishment of a pair bond and nest construction did not inhibit cannibalism of foreign eggs. Second, in experiment 2 we removed eggs from parents for various durations and showed that the act of spawning and the presence of the parents' own brood nearly always maintained care and inhibited cannibalism. Third, parents did not discriminate between their own and foreign broods of eggs or hatched young when supplied with complete or with half-cross-fostered young (experiments 3 and 4). Atypically, across all experiments cannibalism was mostly performed by the female. Taken together, our results trace the behavioural transition from egg consumer to egg carer in this biparental species and expand our understanding of cannibalism to biparental species.

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The consumption of one's own offspring has often been considered a maladaptive behaviour. However, this behaviour is both taxonomically widespread and in some species is a common phenomenon (Bartlett, 1987; Clutton-Brock et al., 2001; FitzGerald, 1992; Fowler & Hohmann, 2010; Manica, 2002b; Mociño-Deloya, Setser, Pleguezuelos, Kardon, & Lazcano, 2009; Smith & Reay, 1991; Tokuyama, Moore, Graham, Lokasola, & Furuichi, 2017). Cannibalism is common because (1) eggs/offspring are small and are often similar in size to prey items taken by adults and (2) eggs have high nutritive value and are typically deposited in a single spatial location in the vicinity of nonbreeding adults (Dominey & Blumer, 1984). While these explanations may help us understand why adults might cannibalize the young belonging to other individuals, the question remains why natural selection would ever favour

parents consuming their own young. Rohwer (1978) was the first to consider such filial cannibalism as an adaptive strategy that could maximize lifetime reproductive success. When ending the current breeding attempt by consuming part of the brood, the cannibal can benefit by improving its own survivorship and future reproduction. By consuming some of the offspring under their care, a male parent may be able to stay longer at the breeding or nesting sites, attract more mates or even care better for the remaining offspring (Gomagano & Kohda, 2008). In contrast, the higher gamete replacement costs mean that females should be less predisposed to filial cannibalism (FitzGerald, 1992).

Several factors are known to influence the cost/benefit ratio of parental care and therefore can increase or decrease the probability of filial cannibalism. (1) Brood size: total filial cannibalism (consuming the entire brood) may be more common when the brood is especially small because the net benefit of raising offspring increases with brood size (Kramer, 1973; Mrowka, 1987; Petersen & Marchetti, 1989; Schwanck, 1986; Sikkil, 1994; Manica, 2002a). (2) Age of the brood: total filial cannibalism usually occurs more frequently early in the caring period, thus minimizing the loss of

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time and resources spent on caring (Lavery & Keenleyside, 1990; Manica, 2002a; Petersen & Marchetti, 1989; Schwanck, 1986; Takegaki, Yoshimoto, & Matsumoto, 2011; Vallon & Heubel, 2016; but see Klug & Lindström, 2008). (3) Energy reserves: total or partial filial cannibalism occurs more often when caring individuals have few alternative foraging opportunities and their body condition is severely reduced as a consequence of care (Kvarnemo, Svensson, & Forsgren, 1998; Marconato, Bisazza, & Fabris, 1993; Okuda & Yanagisawa, 1996a; but see Bose, Kou, & Balshine, 2016; Bose, McClelland, & Balshine, 2016). (4) Mate availability: the probability of total and partial filial cannibalism is expected to increase when additional mates are abundant because replacement broods are possible (Myint, Takeyama, Okuda, Ohnishi, & Kohda, 2011; Okuda & Yanagisawa, 1996b; but see Deal & Wong, 2016). (5) Relatedness: parentage uncertainty is thought to increase the degree of filial cannibalism because genetic relatedness to young also strongly influences the cost:benefit ratio of care and there are few benefits to be gained from raising offspring that are not your own (Bose, Kou et al., 2016; Bose, McClelland et al., 2016; Frommen, Brendler, & Bakker, 2007; Lissåker & Svensson, 2008; Neff & Sherman, 2002).

For parents to adjust their parental behaviour in relation to the costs and benefits of care outlined above, they must be able to assess offspring quantity, quality and identity as well as their social environment. Many studies have demonstrated that certain species are capable of assessing offspring number and quality (Koskela, Juutistenaho, Mappes, & Oksanen, 2000; Lavery & Keenleyside, 1990; Rytönen, 2002). While some studies have shown that animals adjust their parental effort depending on cues of relatedness, other studies have not found support for this idea (Riehl, 2012; Ringler, Pašukonis, Ringler, & Huber, 2016; Sefc, Mattersdorfer, Sturmbauer, & Kobl Müller, 2008; Stiver & Alonzo, 2009; Vallon, Anthes, & Heubel, 2016). Neff and Sherman (2002) partly resolved this discrepancy by showing theoretically that animals should adjust their parental effort but will do so only if there is a cue of relatedness that reliably predicts the reproductive value of young and can override their innate predisposition to care. Therefore, individuals require both information about relatedness and the cognitive ability to assess it. Such kin recognition cues can be visually, acoustically or chemically based (Barry & Göth, 2006; Green, Mirza, & Pyle, 2007; Le Vin, Mable, & Arnold, 2010; Neff, 2003; Okamoto, Shirasu, Fujita, Hirasawa, & Touhara, 2016; Pfefferle, Ruiz-Lambides, & Widdig, 2014) and can come directly from offspring themselves, or be indirect such as nest location or site attachment (Bose, Kou et al., 2016; Bose, McClelland et al., 2016; McKaye & Barlow, 1976; Mínguez, 1997).

Before an individual begins to care, it must first mate and thereafter go through a series of different physiological and behavioural states beginning with finding or attracting a mate and often establishing a pair bond with its breeding partner. Many animals will construct a nest or breeding shelter, and once mating is complete this is followed by the parental and caring phase and finally the individual will revert to the nonbreeding/noncaring state; this cycle repeats every time a breeding attempt occurs. Although many studies have been conducted on cannibalism, we still know little about which factors initiate, maintain and terminate the parental state (Bose, Kou et al., 2016; Bose, McClelland et al., 2016; Frommen et al., 2007; Green et al., 2007; Luzar, Schweizer, Sakaluk, & Steiger, 2017; Moreno, 2012; Ringler et al., 2016; Van Iersel, 1953).

To address which factors initiate, maintain and terminate parental care we studied *Neolamprologus caudopunctatus*, a biparental caring cichlid fish from Lake Tanganyika. Both parents actively defend a breeding cavity containing eggs and young and jointly guard the free-swimming young for up to 40 days (Ochi &

Yanagisawa, 1999). While breeding *N. caudopunctatus* are diligent parents, nonbreeding individuals are voracious cannibals (F. C. Schaedelin & F. Cunha-Saraiva, personal observation). We conducted four experiments to examine the factors influencing the transition from cannibal to caring parent in this species. In experiment 1 we investigated whether an established male–female pair bond and nest construction are sufficient to inhibit cannibalism, by giving pairs at various stages in the breeding cycle a foreign brood. We predicted that pair-bonding and nest-building activities would be sufficient to initiate care and prevent cannibalism of a foreign brood. In experiment 2 we investigated whether the presence of eggs maintains the parental state and inhibits cannibalism. Eggs were removed from parents for various durations and then returned. We predicted that the longer the duration of egg removal, the higher the frequency of filial cannibalism. Finally, we used a cross-fostering design in experiments 3 and 4 to investigate whether parents recognize and avoid cannibalizing their own young. We predicted that parents would be able to discriminate between their own and foreign hatched young (because of odour cues emanating from offspring) but would not necessarily be able to distinguish between their own eggs and foreign eggs, because egg casings may prevent the release of chemical cues needed to assess kinship.

METHODS

Study Animals and Housing Conditions

Neolamprologus caudopunctatus is a socially and genetically monogamous cichlid fish endemic to Lake Tanganyika, Africa (Ochi & Yanagisawa, 1999). Breeding pairs are sexually monomorphic, and provide biparental care (Ochi & Yanagisawa, 1999). Colonies contain 5–100 breeding pairs, with a median nearest-neighbour distance of 65.76 cm (Schaedelin, Dongen, van, & Wagner, 2012). Both female and male breeders actively participate in building the breeding cavity by excavating under stones or by using existing rock crevices or gastropod shells, in which they spawn and care for young (Ochi & Yanagisawa, 1999). Each breeding pair defends its own breeding cavity containing their eggs and larvae and then guards the free-swimming young for up to 40 days (Ochi & Yanagisawa, 1999). Defence of young is targeted most frequently at conspecific nonbreeders (both juveniles and adults; Ochi & Yanagisawa, 1999), which consume young (F. C. Schaedelin & F. Cunha-Saraiva, personal observation). In the experiments described below, we used juveniles (30–45 mm, standard length, SL) as both territorial intruders and potential threats to eggs and young. We used a total of 256 adult (128 males and 128 females) wild-caught *N. caudopunctatus*, all collected at the most southern tip of Lake Tanganyika, Zambia, Africa. Each fish was measured for standard length (from the tip of the longest jaw to the end of the caudal peduncle; mean \pm SD for males: 52.98 \pm 0.63 mm; for females: 46.50 \pm 0.45 mm), total length (TL, males: 64.68 \pm 0.58 mm; females: 56.99 \pm 0.51 mm) and body mass (*M*, males: 3.85 \pm 0.36 g; females: 2.72 \pm 0.31 g). Fish were fed daily with frozen food (a mixture of *Artemia*, *Cyclops* and *Daphnia* species plus red mosquito larvae) and with tropical fish flakes. Tanks were maintained at a constant water temperature of 26 \pm 1 °C under a 12:12 h light:dark cycle.

General Procedures and Experimental Set-ups

Fish were held in mixed-sex stock 400-litre and 160-litre aquaria equipped with a heater, a filter and a 5 cm sand layer. Stock tanks contained an approximate 1:1 sex ratio and six to eight half flowerpots as potential breeding sites. After individuals formed

pair bonds in these tanks, pairs were removed and used in the experiments described below. We allowed free mate choice, since preliminary tests suggest that artificially composed or forced pairs will not engage in breeding as quickly or as successfully (F. Cunha-Saraiva, personal observation). Each pair was then placed in a 45-litre experimental aquarium equipped with 2 cm of sand, and provided with a breeding shelter consisting of a 10 × 10 cm wide PVC slate folded into a triangle, a heater and a filter sponge. Shelters were then checked daily for eggs. A clear acetate sheet lined each breeding shelter allowing us to easily collect, count and photograph the eggs. Pairs were randomly assigned to one of the following four experiments. Fish were not reused between experiments, except for the 24 pairs used in experiment 1 which were also used in experiment 2.

Experiment 1: Does Pair Bonding Inhibit Cannibalism?

We conducted this experiment using 24 pairs, each with a shelter lined with an acetate sheet. We confirmed that all pairs were bonded via detailed observations and noting progress on nest construction, which always precedes spawning. We used 12 pairs that had not yet spawned and 12 pairs that had already spawned. The 12 pairs that had already spawned had their own eggs on an acetate sheet removed for less than 5 min and then these eggs were returned to their shelters while the 12 nonspawning pairs had new acetate sheets placed in their shelters containing an unrelated brood of eggs on it. One hour later, we inspected all the acetate sheets and recorded the absence or presence of the brood. In all cases in which eggs were cannibalized, parents consumed the entire brood of eggs.

Experiment 2: Does Spawning Maintain the Parental State?

We used 64 pairs that had already spawned in this experiment. The treatment was assigned randomly. All pairs had their eggs removed for either 5 min (control pairs), 3 h, 9 h or 15 h (with 16 pairs in each treatment group). During the removal, an egg-free acetate sheet lined the brood chamber. Removed broods of eggs were temporarily housed in aquaria with an airstone placed underneath the brood to ensure proper development. We did not observe any fungal growth on the eggs during or after the removals. Following the treatment duration, the brood of eggs was returned to the brood chamber and to the parents. Before and after the brood of eggs was returned, we conducted a 10 min behavioural observation followed by a nest defence assay (see below). This defence assay was used to assess pair stability and willingness to care for the eggs. For each treatment, brood size (number of eggs) and change in brood size were quantified based on digital photographs taken of the brood just before and 1 h after the manipulation. The NIH's ImageJ analysis program (Schneider, Rasband, & Eliceiri, 2012) was used to quantify egg number.

Experiment 3: Do Parents Avoid Cannibalizing Their Own Eggs?

We used a total of 48 pairs in this experiment. We cross-fostered broods so that experimental pairs had 0%, 50% or 100% of their brood replaced with the brood of another pair with eggs of the same age. Broods were always at the egg stage. All broods were halved by cutting the acetate sheet in half. We then fixed two half sheets together with tape. In the 0% cross-fostered treatment we used the original halves, in the 50% cross-fostered treatment we exchanged one half with that of another brood at the same stage of development and in the 100% cross-fostered treatment we exchanged both halves. Additionally, we ensured that in the case of the partial cross-fostered treatment (50%) each half had an equal

brood size. This cutting and taping procedure lasted about 5 min for all treatments and all broods were never out of the water for more than 5 min. We used 16 pairs in each treatment group. Before and after the experimental manipulation we conducted a 10 min behavioural observation on the pair followed by a nest defence assay (see below) to assess the pair stability and willingness to care. A digital photograph was taken of each brood just before and 1 h after the manipulation. The number of eggs remaining was quantified using NIH's ImageJ analysis (Schneider et al., 2012). In the 50% cross-fostered treatment, we counted foreign and own eggs remaining separately.

Experiment 4: Do Parents Cannibalize Foreign Hatched Young?

To test whether hatching decreased (or increased) the cannibalism rates of cross-fostered young, we cross-fostered broods of freshly hatched larvae (within the first week after hatching) so that all the experimental pairs had ca. 100% of their brood replaced with the brood of another pair. We used a total of 16 pairs in this experiment and broods were always at the hatched young stage but were not yet free swimming. We inspected all breeding shelters 1 h and 24 h later and recorded the absence or presence of young. If parents are able to smell their own hatched young then we expected an increase in whole brood cannibalism of cross-fostered broods of hatched young.

Behavioural Assays and Scoring

In experiments 2 and 3, pairs were observed before and after the manipulations, with each recording session of 10 mins starting after a 2 min habituation period. We divided parental behaviour into three categories: (1) nest maintenance, which included any acts of digging and/or sand transport away from the nest, (2) nest defence, which included any approach and fin spreading towards the juvenile intruders and (3) egg care, which included nest cavity visits, egg cleaning and fanning. We also recorded any aggressive and submissive behaviours performed towards partners. A full description of all the behaviours recorded can be found in Table 1, which is an ethogram specifically designed for this cichlid species. The nest defence assay consisted of placing a transparent Plexiglas cylinder containing three conspecific juveniles into each pair's tank. The nest defence assay lasted for 2 min, starting as soon as one of the breeding pair performed an aggressive display or act towards the cylinder (average time until first interaction with intruder: 1.59 ± 0.09 min). If no aggression ensued after 10 min the trial was stopped and the cylinder removed. All aggressive behaviours towards the juveniles and between the breeding pair were recorded.

Statistical Analysis

All analyses were performed using R statistical software (R Development Core Team, 2016). To determine whether pair-bonding and nesting activities inhibit cannibalism (experiment 1), all egg cannibalism events for both spawning and nonspawning experimental pairs were tallied and analysed using a Fisher's exact test. To determine whether the presence of eggs in the nest maintains the parental state (experiment 2), the occurrences of cannibalism in each egg removal treatment (5 min, 3 h, 9 h and 15 h) were analysed using a Fisher's exact test for count data and, using the RVAideMemoire package (Maxime, 2017), pairwise comparisons were conducted using both `fisher.test` and `fisher.multcomp` functions. To determine whether parents recognize and avoid cannibalizing their own eggs (experiment 3), we tallied all egg cannibalism events for each cross-fostered treatment (0% =

Table 1
The ethogram used to score the behaviours of *N. caudopunctatus* during parental care observations and the intruder test

Type of behaviour	Description
Aggression (physical attacks)	
Ram	Focal fish touches another fish with its head or mouth region, jaws are closed
Forced displacement	Focal fish approaches another fish, but opponent moves away
Open mouth approach	Focal fish approaches another fish with an open mouth
Mouth wrestle	Focal fish and its opponent lock jaws and push against one another in a reverse tug-of-war. Also known as mouth-fight
Chase	Focal fish quickly darts towards another fish and follows this fish (swims after another for several body lengths)
Aggression (displays)	
Fin spread	Focal fish spreads its fins including ventral fins. This can be done while next to or while circling the opponent, or by displaying its fins parallel to the opponent, which is also called lateral or parallel display
Frontal display	Focal fish spreads its opercula and lower jaw. Mostly in combination with fin spread and/or approach. Also known as opercula flare
Approach	Focal fish approaches opponent with closed jaws, as if about to ram, but without any physical contact
Head down	Focal fish lowers its head and raises its tail, sometimes in front of or alongside its opponent. This display is shown during courtship and territory defence
Bars	Focal fish shows black stripes on its body and has black coloured eyes, mostly in combination with fin spread
Head down and bars	Focal fish lowers its head and raises its tail with fin spread, black coloured eyes and black stripes on its body, sometimes in front of or alongside its opponent. Also shown during courtship and territorial patrol
S-bend	Focal fish bends its body laterally in an S-curve towards another fish
Pseudo-mouth wrestle	Both fish move back and forth while facing each other, as if about to mouth wrestle, but no physical contact is established
Submission (flees)	
Flee	Focal fish quickly swims away for more than one body length
Submission (display)	
Set back/Avoid	Focal fish retreats or displaces slowly from another fish
Tilt	Focal fish tilts its body towards opponent, exposing the belly
Locomotion	
Sit	Fish touches the ground with its abdomen
Cavity parental care	Fish remains inside the shelter
Egg fanning	Focal fish fans the eggs using its pectoral fins
Egg cleaning	Focal fish touch the eggs with its mouth but removes only fungus which ensures proper development of eggs
Brood chamber	Focal fish enters the brood chamber
Sand transport	Focal fish takes a mouthful of sand and swims to either the brood chamber or to an area near the brood chamber before spitting it out. Usually this is done to construct a sand wall around the brood chamber that serves as further protection for the offspring (also called Out-In)
	Focal fish takes a mouthful of sand inside the brood chamber or near the brood chamber, swims away from it and spits it out. Usually is done to construct a cavity to breed in (also called In-Out)
	Focal fish takes a mouthful of sand and swims to another place away from the brood chamber where it spits the sand out (also called Out-Out)
Egg cannibalism	
Egg eating	Focal fish swims into the cavity, grabs an egg with its mouth and eats it

This ethogram is adapted from one designed for *Neolamprologus pulcher* (Hick, Reddon, O'Connor, & Balshine, 2014; Sopinka et al., 2009).

control, 50% = partial cross-fostered treatment and 100% = complete cross-fostered treatment) and analysed these using a Fisher's exact test for count data using `fisher.test`.

To determine whether parents recognize and avoid cannibalizing their own hatched young (experiment 4) we analysed all cannibalism events using an exact binomial test using the `binom.test` function. In experiment 3 a repeated measures ANOVA was used to compare brood size before and after the manipulation and to assess whether experimental pairs were able to discriminate between foreign and own eggs. Brood size was used as the dependent variable, while experimental phase (before and after manipulation), brood origin (own versus foreign) and the interaction of the two were used as independent variables and pair identity was a random effect. Finally, using all the experiments together and all instances where egg cannibalism occurred, data distribution-dependent tests (Dalgaard, 2008) were used to assess the potential effect of offspring age, brood size, parental body condition (Fulton's condition factor (Fulton, 1911), which was calculated as $K_{\text{parents}} = K_{\text{male}} + K_{\text{female}} = 100 \times M_{\text{male}}/SL_{\text{male}}^3 + 100 \times M_{\text{female}}/SL_{\text{female}}^3$), and within-pair aggression on the propensity to cannibalize.

For each experimental individual, a parental care score was calculated, comprising the sum of all observed parental care behaviours (including nest defence, egg care and nest maintenance). To assess the potential behavioural effect of the different treatments, a generalized linear mixed model with a Poisson error

distribution was performed using the `glmer` function from the `lme4` package (Bates, Maechler, Bolker, & Walker, 2015). In experiment 2, the parental care score was used as a dependent variable in the model, while treatment (5 min, 3 h, 9 h and 15 h), experimental phase (before and after manipulation) and sex were used as independent variables, pair identity was a random effect and brood size a covariate. In experiment 3, the parental care score was used as a dependent variable in the model, while treatment (0% = control, 50% = partial cross-fostered treatment and 100% = complete cross-fostered treatment), experimental phase (before and after manipulation) and sex were used as independent variables, pair identity was a random effect and brood size a covariate. Whenever brood size was not significant it was removed from the model. Final models were validated and tested for overdispersion using the `dispersion.glmer` function from the `blmeco` package (Korner-Nievergelt et al., 2015).

All GLMM models were corrected for overdispersion, by using a negative binomial distribution (Zuur, Ieno, Walker, Saveliev, & Smith, 2009).

Ethical Note

The experimental procedures were discussed and approved by the University of Veterinarian Medicine Vienna, Austria ethics and animal welfare committee and are in accordance with Good Scientific Practice guidelines and national legislation (ETK-05/10/2015).

RESULTS

Experiment 1: Does Pair Bonding Inhibit Cannibalism?

Pair formation and nest construction were not sufficient to inhibit egg cannibalism, but spawning was. All 12 pairs that had not yet spawned ate the entire brood provided, but none of the 12 spawning pairs did (Fisher's exact test for count data: $P < 0.0001$).

Experiment 2: Does Spawning Maintain the Parental State?

The probability of whole brood filial cannibalism increased with the duration of the brood removal (Fig. 1; Fisher's exact test for count data: $P < 0.0001$). No eggs were eaten when the eggs were removed for 5 min or for 3 h. However, 31% of the parents engaged in total brood filial cannibalism when eggs were removed for 9 h, and 69% of the parents did so after 15 h. Of the 11 cannibalized broods in the 15 h brood removal treatment, only one brood was eaten by the male, eight were eaten by the female alone, one brood by both the male and female, and in one case we could not determine who the cannibal was because the brood was consumed outside the behavioural observation period.

Prior to the brood removal manipulations, experimental pairs performed on average 15 ± 1.1 (mean \pm SE) parental care behaviours (including nest maintenance, egg care and nest defence) during the 10 min behavioural observation periods. Females performed more parental behaviour than males (Table 2). The 15 h removal led to a reduction in parental care behaviour, but no significant reduction in care was observed following the 3 and 9 h brood removal treatments (Table 2).

Experiment 3: Do Parents Avoid Cannibalizing Their Own Eggs?

Breeding pairs caring for young appeared unable or insufficiently motivated to discriminate between their own eggs and foreign eggs. There was no significant decrease in brood size when pairs were given 50% of their own young and 50% foreign young (Table 3). However, while whole brood cannibalism did not occur in the control (100% own eggs) or in the 50% foreign eggs partial

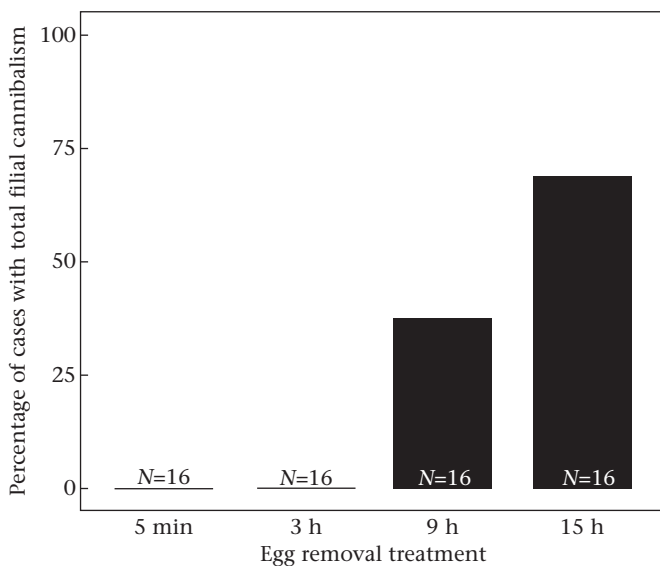


Figure 1. Percentage of confirmed cases of total filial cannibalism in each brood removal treatment. Pairwise comparisons: 5 min versus 3 h: $P = 1.0$; 5 min versus 9 h: $P = 0.026$; 5 min versus 15 h: $P = 0.0002$.

Table 2

Generalized linear mixed model analysis of parental care behaviour following different removal durations

Factors	Estimate \pm SE	z	P
Pair ID	2.91 \pm 0.11	26.42	<0.001
Treatment			
Control vs 3 h	0.10 \pm 0.15	0.66	0.50
Control vs 9 h	0.14 \pm 0.15	0.91	0.35
Control vs 15 h	-0.43 \pm 0.15	-2.80	0.005
Experimental phase			
Before vs after manipulation	-0.02 \pm 0.03	-2.80	0.38
Sex	-0.64 \pm 0.03	-19.01	<0.001

Significant P values are shown in bold.

fostering treatment, 25% (four of 16) pairs that received 100% foreign eggs cannibalized the whole brood (Fig. 2; Fisher's exact test for count data: $P = 0.02$).

Before the egg removal manipulations, experimental pairs performed on average 15.5 ± 1.2 (mean \pm SE) parental care behaviours (including nest maintenance, egg care and nest defence) during the 10 min behavioural observation periods. As in the last experiment, females performed more parental care behaviour than males (Table 4). Complete cross-fostering (100%) resulted in a reduction in parental care, but no significant reduction in care was observed in the control or partial fostering (50% cross-foster) treatments (Table 4). There was a significant increase in parental care behaviour after the manipulation (Table 4). After the cross-fostering manipulations, experimental pairs performed on average 20.8 ± 1.7 (mean \pm SE) parental care behaviours during the 10 min behavioural observation periods.

Experiment 4: Do Parents Cannibalize Foreign Hatched Young?

In 15 of 16 cases, we did not detect any reduction in the number of larvae in cross-fostered broods (binomial test: $P < 0.0001$).

Factors Influencing Filial Cannibalism

Eggs of *N. caudopunctatus* typically hatch on the third day after spawning at 25/26 °C (F. Cunha-Saraiva, personal observation). In the experiments described above, eggs varied in age between 1 day ('young eggs') and 2 days or older ('older eggs'). Although both young and older eggs were eaten or accepted by pairs throughout these four experiments, overall older eggs were more likely to be cannibalized than younger eggs (Wilcoxon test: $W = 207.5$, $N = 32$, $P < 0.001$; Fig. 3a). Across experiments, brood size ranged from 42 to 257 eggs. Brood size was an important predictor for filial cannibalism; smaller broods were more often cannibalized than larger broods (t test: $t_{30} = -2.83$, $P = 0.008$; Fig. 3b). Although low energy reserves are known to increase the likelihood of egg cannibalism (Manica, 2002b), in our study parental body condition did not influence filial cannibalism (Wilcoxon test: $W = 143$, $N = 32$, $P = 0.57$; Fig. 3c). Finally, conflict between the sexes can lead to the termination of parental care (Palombit, 2015); however,

Table 3

Repeated measures ANOVA

Factors	df	Mean square	F	P
Experimental phase	1	21.9	0.028	0.86
Brood origin	1	54	0.068	0.79
Interaction	1	36.2	0.046	0.83
Error (Pair ID)	13	502.2		

Potential factors influencing brood size: egg origin = own and foreign eggs; experimental phase = before and after manipulation.

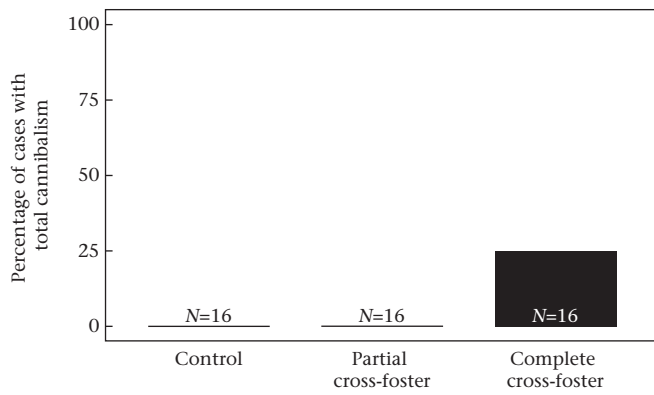


Figure 2. Percentage of cases where parents performed whole brood cannibalism across the cross-fostered treatment groups.

Table 4
Generalized linear mixed model analysis of care behaviour

Factors	Estimate±SE	z	P
Pair ID	3.14±0.15	20.59	<0.001
Treatment			
Control vs 50%	−0.28±0.18	−1.52	0.12
Control vs 100%	−0.39±0.20	−1.93	0.05
Experimental phase			
Before vs after manipulation	0.25±0.11	2.29	0.02
Sex	−0.59±0.11	−5.33	<0.001

Intercept is the individual identification for each experimental pair (random effect). Treatment: control (no cross-fostering), 50% (partial cross-fostering) and 100% (complete cross-fostering). Significant *P* values are shown in bold.

in our study within-pair aggression did not influence rates of filial cannibalism (Wilcoxon test: $W = 137$, $N = 32$, $P = 0.73$; Fig. 3d).

DISCUSSION

Our study shows that the presence of eggs in the breeding cavity is an important cue maintaining the parental state. Increasing the time that eggs were absent from a nest increased the likelihood of egg cannibalism, with a long duration without eggs (e.g. 15 h) resulting in a dramatic decrease in parental care. *Neolamprologus caudopunctatus* parents did not discriminate between their own and foreign eggs or hatched young, continuing to provide care for both. However, the amount of parental care behaviour did decrease when parents received a completely foreign brood of eggs. Egg age and brood size were reliable predictors of egg cannibalism; however, neither parental body condition nor within-pair aggression was linked to cannibalism.

In our study, foreign broods of eggs were immediately devoured by nonspawning pairs, but spawning pairs never cannibalized broods. Our results are in line with what has been found in other caring species (Smith & Reay, 1991) such as *Trichogaster trichopterus* (Johns & Liley, 1970; Kramer, 1973) and the closely related *Neolamprologus pulcher* (von Siemens, 1990). In *N. pulcher*, the presence of eggs is an important cue that maintains the parental state; however, a brief removal of the brood (4 h after spawning) shut down parental care and induced egg cannibalism (von Siemens, 1990). Foreign broods of eggs were immediately consumed by the female *N. pulcher* while males continued to care for them (von Siemens, 1990). In *N. caudopunctatus*, the presence of eggs is also an important cue. Pairs that had their own brood of eggs removed for 9 h or 15 h ate eggs with a reduction in parental care behaviour following a 15 h removal.

Parental care behaviour is initiated and maintained by a shift in the endocrinological state of the parent. Prolactin is considered an important parental hormone in mammals, birds and fish (Angelier & Chastel, 2009; Bachelot & Binart, 2007; Whittington & Wilson, 2013). The start of the incubation behaviour and subsequent development of the brood patch in bantam hens, *Gallus domesticus*, is the result of an increase in prolactin levels (Sharp, Macnamee, Sterling, Lea, & Pedersen, 1988). Loss of visual and tactile stimuli with the clutch removes the stimulatory control of prolactin, resulting in the termination of incubation (Sharp, Scanes, Williams, Harvey, & Chadwick, 1979, 1988). In our study it is possible that a long period without eggs (15 h) might have triggered an irreversible hormonal change (Tacon, Baroiller, Bail, Prunet, & Jalabert, 2000), for example lowered prolactin may have reversed the parental state especially with females reverting to their pre-spawning state, and egg consumption. Further work is needed to test this idea and quantify prolactin levels in both sexes during the different stages of the reproductive cycle.

Our results suggest that parents are influenced by the reproductive value of offspring, which depends on several factors including brood size and age, and the parents' energy reserves. When parental condition is low and brood size is small, parental care may be highly costly because it reduces the possibility of future mating, growth and survival (Marconato et al., 1993; Rohwer, 1978). Egg age was an important predictor of filial cannibalism in our study. However, our results were not in line with the expectation that filial cannibalism would occur more frequently early in the cycle to minimize the loss of resources (Mehlis, Bakker, Engqvist, & Frommen, 2010; Vallon & Heubel, 2016). In *N. caudopunctatus* the incubation period is only 3 days (F. Cunha-Saraiva, personal observation). Previous studies that have examined the influence of egg age on filial cannibalism were conducted in species that had longer incubation periods lasting from 5 to 23 days (Salfert & Moodie, 1985; Sikkil, 1994; Vallon et al., 2016). In species with long incubation periods, egg cannibalism can be advantageous when parental condition is low and partial filial cannibalism is an option, or when the age of the eggs can be used to assess paternity (Mehlis et al., 2010). In our experiments, most cannibalized broods of eggs were at least 2 days old, when egg care is almost complete. However, parents continue to care for hatched young for another 3–4 weeks, which means that the major part of the parental investment is still ahead. It might therefore be an insignificant time delay if the parents ate 2- or 3-day-old eggs because by doing so they may save time and energy for a renewed breeding attempt. Also, by eating the eggs, the female can quickly allocate the consumed energy for future broods, shortening the time between broods (Klug & Lindström, 2008).

Of the broods of eggs cannibalized, 73% were consumed by the female. Males (but not females) were expected to be the cannibalistic sex (FitzGerald, 1992; Manica, 2002b), an assumption based on the high reproductive investment in eggs by females (Manica, 2002b; Palombit, 2015; Royle, Smiseth, & Kölliker, 2012; Schwanck, 1986). Females typically invest more in gametes than males, and brood size production depends on female body condition, whereas male body condition does not influence brood size (Dominey & Blumer, 1984; FitzGerald, 1992; Manica, 2002b). Although in many species, males are cannibalistic (Lavery & Keenleyside, 1990; Schwanck, 1986), it remains unclear how common female cannibalism is. Termination of parental care via cannibalism by females has also been reported in other taxa: bonobo, *Pan paniscus* (Fowler & Hohmann, 2010), meerkat, *Suricata suricatta* (Culot et al., 2011), lance-headed rattlesnake, *Crotalus polystictus* (Mociño-Deloya et al., 2009) and European pied flycatcher, *Ficedula hypoleuca* (Moreno, 2012). Female filial cannibalism is often associated with increased environmental stress or

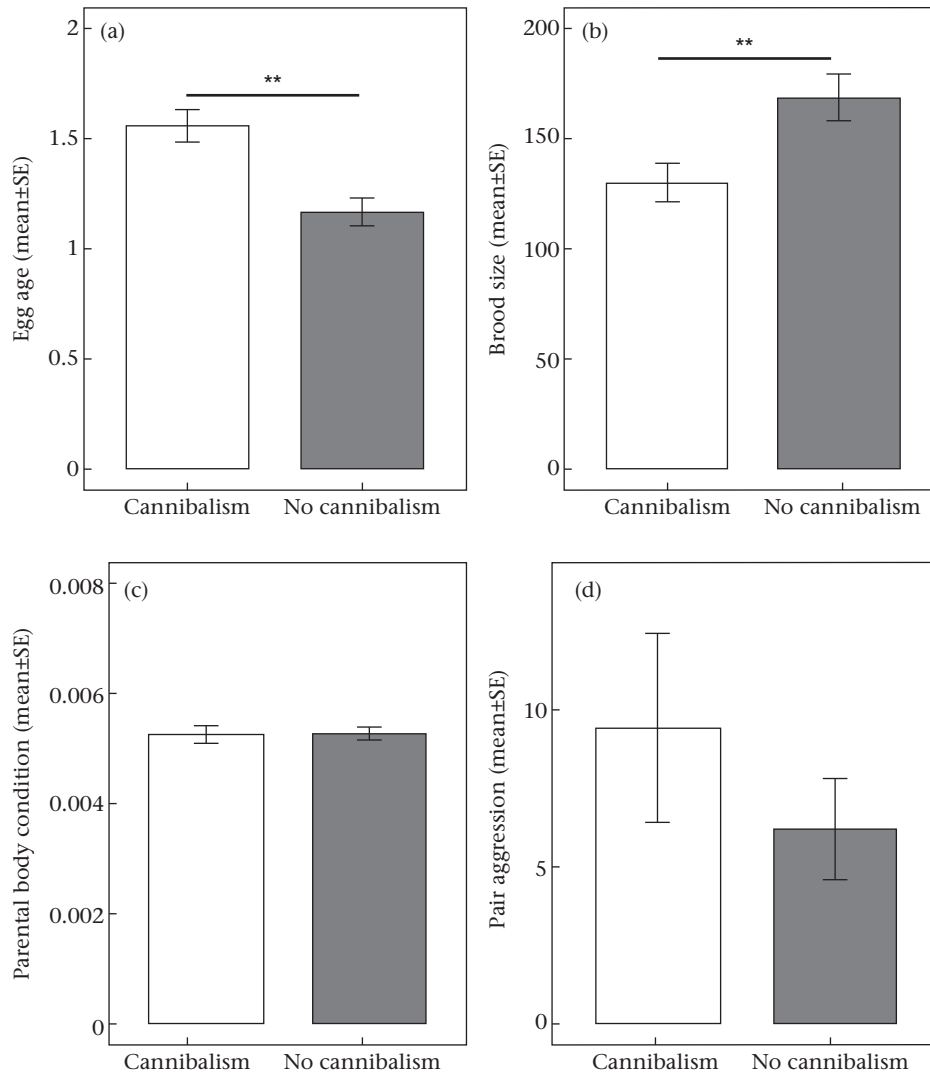


Figure 3. Influence of (a) egg age, (b) brood size, (c) parents' body condition and (d) pair aggression on egg cannibalism. Grey bars: nests with egg cannibalism; white bars: nests without egg cannibalism. ** $P < 0.01$.

reduced food provisioning (Culot et al., 2011; Mociño-Deloya et al., 2009). In *N. caudopunctatus*, females and males defend the young and maintain the nest together. However, it is the female that actively attends the cavity and regularly cleans and fans the eggs. In this study, we observed that females monopolized the breeding shelter during egg care. Females prevented males from entering the breeding shelter and were aggressive towards their mates whenever they tried to enter or successfully entered the shelter. Therefore, it is likely that the female has more opportunities to cannibalize and so holds the power to decide when it is advantageous to terminate or continue investing in the current brood.

Acceptance of a foreign brood of eggs could indicate that kin recognition capabilities might never have evolved or might be impaired due to an absence of chemical cues (Bose, Kou et al., 2016; Bose, McClelland et al., 2016; Keller-Costa, Canário, & Hubbard, 2015). Neff (2003) showed that when perceived paternity is reduced experimentally at the egg stage, caring male bluegill sunfish, *Lepomis macrochirus*, reduce their parental investment. However, after the eggs hatch and true paternity can be assessed more accurately based on chemical cues emanating from the hatched young, the caring male re-establishes its high levels of parental care. We also recorded a reduction in parental care (Table 4) in

broods of eggs that had been completely cross-fostered; these broods of foreign young received less care than control broods of eggs that contained the pair's own young.

Although parents reduced their parental care to foreign cross-fostered broods of eggs, they did not significantly reduce care to cross-fostered broods of foreign hatched young. Cannibalism occurred in only one of the 16 hatched young trials. Thus, *N. caudopunctatus* appears not to discriminate between kin and nonkin. Perhaps kin recognition is unnecessary in this species. This may be the case for two reasons: (1) *N. caudopunctatus* parents have been shown to be both socially and genetically monogamous (Schaedelin, Dongen, van, & Wagner, 2015), which means that offspring parentage is not likely to be in question, and (2) breeding pairs commonly adopt foreign fry (Schaedelin et al., 2012), which is potentially beneficial by diluting predation risk (Wisenden & Keenleyside, 1992, 1994).

In conclusion, *N. caudopunctatus* cannibalize their own young and do so depending on the size and age of the brood. This is among the first studies to show that females, as well as males, are cannibalistic (Jindal, Bose, O'Connor, & Balshine, 2017; Lavery & Keenleyside, 1990; Schwanck, 1986). Our results enhance our knowledge of filial cannibalism by expanding the study of this

phenomenon to a biparental species and set the stage for investigating proximate mechanisms underlying the behavioural transition from cannibal to caregiver.

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