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Mate switching as a function of mate quality in the convict cichlid, Cichlasoma nigrofasciatum (Pisces: Cichlidae)

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Mate Switching as a Function of Mate Quality in the Convict Cichlid,...

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Mate switching as a function of mate quality in the convict cichlid, *Cichlasoma nigrofasciatum* (Pisces: Cichlidae)

by

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Abstract. Mate switching and competition for breeding sites were examined between mated pairs of monogamous convict cichlids as a function of mate quality (size). A mated pair was established in each half of a 284 l aquarium, an opaque partition separating the two pairs. When the partition was removed, large pairs outcompeted small pairs for access to breeding space. However, misassorted pairs (large males with small females competing with small males with large females) resorted themselves such that the larger male paired with the larger female 46% of the time. The resorted pair, containing the large male, then monopolized the entire aquarium. Resortment resulted both from a preference for a larger mate and the ability of larger individuals to displace their smaller consexual. However, small females, when paired with a large male, often dominated large females and prevented the large female from mating with the large male. The availability of more than one breeding site in the aquarium had no effect on the frequency of resortment.

INTRODUCTION

Many studies attempting to understand divorce in monogamous species have hypothesized that it results from one or both pair members attempting to improve their breeding situation (see Choudhury 1995 for a review in birds). The most inclusive hypothesis predicts that paired individuals should divorce when at least one of the partners gains a better partner or territory. A number of studies in birds were consistent with this hypothesis, although in these studies the female appeared to benefit more than the male. Dhondt & Adriaensen (1994) found that the reproductive success of blue tit females, *Parus caeruleus*, increased after divorce. By removing clutches of the pied flycatcher, *Ficedula hypoleuca*, Lifjeld & Slagsvold (1988) induced female-initiated divorce whereafter females were more likely than males to acquire a new mate. Divorce did not occur when males were of higher quality. In Otter & Ratcliffe's study of black-capped chickadees, *Parus atricapillus*, females deserted their mate to re-pair with neighbouring widower males of higher social rank. An improved breeding situation, potentially determined by assessing past reproductive success or merely present options, seems to be the functional if not the causal explanation of divorce. However, no studies have experimentally manipulated mate quality and tested its effect on the propensity to switch to a better one, while controlling for the confounding influence of past reproductive success.

Using the sexually-dimorphic, substrate-spawning, monogamous convict cichlid fish, *Cichlasoma nigrofasciatum*, I experimentally tested the hypothesis that mate switching should occur when at least one member of a pair is able to obtain a higher-quality mate. Although mate desertion occurs in this serially monogamous species (Wisenden 1994), no studies empirically identify a functional or causal mechanism. Convict cichlids in the field mate assortatively by size

(McKaye 1986), suggesting that some form of mate choice and/or intrasexual competition exists. Females prefer larger males (Noonan 1983), and males should prefer larger females, probably because resource-holding power increases with body size for both males and females. In Texas cichlids, *Cichlasoma cyanoguttatum*, larger males and females defeat smaller individuals in intrasexual combat (Haley 1987) and are thus better able to acquire and defend a breeding territory. In addition, males should prefer larger females, because female fecundity increases with body size in many fish, including cichlids (Sargent et al. 1986). Due to the increase in reproductive success males and females incur by mating with the largest available mate, size is a definitive indicator of reproductive quality. I tested the mate-switching hypothesis by mis-assorting pairs for quality, such that one pair contained a higher-quality male and a lower-quality female than another pair to which it was exposed. I predicted that, when individuals of higher reproductive quality (i.e. larger) were initially paired with mates of lower reproductive quality (i.e. smaller), pairs should resort such that the higher-quality individuals pair with each other.

McKaye (1986) suggested that competition may enhance the benefits of being paired with the largest available mate, because two large individuals may be best able to acquire a breeding territory. As mate switching is time consuming and may delay reproduction (e.g. Coulson 1972; Ens et al. 1993), I also hypothesized that switching to larger mates should become more pronounced when nesting sites become more limited.

METHODS

Adult convict cichlids were purchased from a pet store and maintained in unisexual groups in 473 l stock tanks (25 ± 2°C). Experimental aquaria (284 l at 25 ± 2°C) contained a thin layer of coarse gravel substrate with 1 flower pot (8 cm diameter) in each back corner. The aquaria were divided into 2 cubic compartments of equal volume by an opaque, black, plastic partition that fit securely between the glass but could be easily removed. Fish were taken from the stock tanks and their size measured prior to placing them in the experimental aquaria. The length of the fish from the snout to the end of the caudal fin (SL) was measured to the nearest mm.

One male and one female were placed in each compartment. In the misassorted group (N=46), the larger of 2 males was assigned to the smaller of 2 females in one compartment, and in the other compartment, the smaller male was assigned to the larger female. In the assorted group (N=26), the larger male and female were placed in one compartment, and the smaller male and female were placed in the other. In both groups, males (6.2-11.0 cm SL) were always larger than females (5.0-7.5 cm SL). Intrasexual size differences were between 0.5 and 1.5 cm for males and between 0.5 and 1.0 cm for females. Intersexual size differences never exceeded 3.5 cm. This setup was left for 24 h.

Assessment of pair-bond formation

Pair-bond formation is readily observed if a pair of convict cichlids is presented with an intruder (unpublished data, Triefenbach and Itzkowitz). If a pair-bond has formed, the mated pair will intensify their courtship behaviour in the presence of the intruder and attack the intruder. Thus, in order to operationalize and verify pair formation, a randomly selected male intruder (size range 4.8-5.3 cm SL), smaller than both male and female, was confined in a 250 ml Erlenmeyer flask and placed in the corner of the tank, 30 cm in front of the pot, for 10 min. During this intruder presentation, data was recorded on: 1) aggression towards intruder, i.e. time individuals or pair (individuals within 5 cm of each other) spent nipping at the intruder flask; 2) courtship within pairs, i.e. time pair spent quivering or within 5 cm of each other; 3) time individuals spent occupying or hiding behind the pot; and 4) aggression within pairs, i.e. frequency of nips or chases one partner performed to the other. A pair-bond was considered formed when both partners exhibited courtship and spent at least 60 s nipping at the flask containing the intruder. In a preliminary study, 10/11 pairs that attacked the smaller male intruder spawned subsequently (unpublished data). If adjacent "pairs" failed to exhibit these behaviors within 4 days after setup and within 24 h of each other, the replicate was discarded. Out of 98 attempted replicates, 72 met the criterion of showing pair formation on both sides of the partition within 24 h of each other. Once both pairs had formed within 24 h of each other, the partition between the pairs was removed.

For further analysis, the data from the intruder presentation were used to assess pair compatibility as a function of whether the individuals were closer or further apart in size. I first calculated male-female size differences for each established pair and divided the pairs into 3 groups: similar size (0-0.9 cm difference; N=16), intermediate differences (1.0-1.9 cm difference; N=32) and large differences (2.0-3.5 cm difference; N=27). These 3 groups were then compared for behavioural differences.

Mate-switching experiment under two conditions of breeding site availability

The maintenance of the pair-bonds of the two mating pairs was then examined under two conditions of breeding site availability. In order to limit breeding sites, the two pots were removed and replaced by a single pot in 17 of the assorted and in 28 of the misassorted replicates. For the other 9 assorted and 18 misassorted replicates, the pots were left intact. Fifteen minutes after partition removal, data was recorded for 15 min on the time spent by all individuals engaging in aggressive encounters (chases, frontal displays [an agonistic encounter whereby a fish extends its branchiostegals at another], and mouthfighting), on courtship frequency (quivering and within 5 cm of each other), and on time spent occupying or defending the pot.

Twenty-four hours after removing the partition, the aquarium was typically dominated by a single pair. That pair was identified by the following criteria: both partners monopolized the pot(s) and chased the other two individuals without themselves ever being chased. If subordinate individuals were attacked too vigorously (injured or being chased), they were removed. Pair tolerance was defined as two pairs defending a separate breeding site. In some replicates (N=22), the pairs were allowed to remain together so as to determine whether or not they would spawn.

Mate removal experiment

In order to more closely examine intrasexual competition of one sex at a time, I repeated the same experiment, this time removing one of the individuals. I set up 23 misassorted replicates as described above. Prior to partition removal and replacement of both pots by a single one, I removed either the large female (N=6), the small female (N=5), the large male (N=6), or the small male (N=6). No behavioural data was recorded, but the individuals comprising the dominant pair were determined 24 h later as described above.

Analysis

Interval and frequency data from two treatments were analyzed using the Mann-Whitney rank sum test. Interval and frequency data from more than two treatments were analyzed using a Kruskal-Wallis one-way nonparametric ANOVA. If a significant difference was found in the analysis, specific differences between treatments were isolated with Dunn's test for multiple comparisons. When no significant differences were found between related variables (e.g. mouthfights, frontal displays and chases between males), the data were collapsed into one variable for further analysis (e.g. intrasexual aggression). Ordinal (outcome frequency) data were analyzed using the chi-square test. All computations were performed using the statistical software program, Sigma Stat for Windows, v: 1.0.

RESULTS

Assessment of pair-bond formation (before partition removal)

In accordance with my operational definition of pair-bond formation, all bonded individuals spent at least 60 s attacking the intruder flask together and intermittently courted each other near the bottle and in the pot (Table I). Individuals also spent time alone, either occupying or hiding behind the pot, attacking the intruder, or lingering in a section of the compartment more than 10 cm away from either the pot or the intruder. The 3 groups (similar-sized male and female, intermediate differences, large differences) were significantly different for the number of times the female nipped the male (Fig. 1). Females in the similar-size group performed more nips to their mates than did females in the intermediate difference and large difference groups. Two of the 3 groups were also significantly different for time females spent hiding behind the pot (Fig. 2). Females in the large difference group spent more time hiding than females in the similar-sized group.

Mate switching experiment (after partition removal)

The 15-minute interaction revealed that nest site availability (1 vs. 2 pots) did not affect any of the behaviors examined (Table II). The data for the two levels of this factor (1 and 2 pots) were consequently collapsed for further analysis between the two assortment groups (Table III). There were differences in intersexual aggression and courtship between the two assortment groups. Large females chased small males more in the assorted than in the misassorted group, that is, when their initial partner was the large male. Large males chased large females more in the misassorted than in the assorted group and chased small females more in the assorted than in the misassorted group. A within-treatment analysis revealed that large males in the assorted group chased small females significantly more than large females (Mann-Whitney rank sum test: T=222, N=20, P<0.02; Fig. 3), whereas within the misassorted group, there was no difference between the times large males chased either female (Mann-Whitney rank sum test: T=184, N=22, NS; Fig. 3). Similarly, the large males' courtship with small females was more frequent in the misassorted than in the assorted group (Fig. 4), whereas their courtship with large females was more frequent in the assorted than in the misassorted group. Within the assorted group, large males' courtship with large females occurred significantly more often than with small females (Mann-Whitney rank sum test: T=115, N=20, P<0.001; Fig. 4), whereas in the misassorted group, there was no significant difference between the large males' courtship with either female (Mann-Whitney rank sum test: T=196, N=22, NS; Fig. 4).

Twenty-four hours after partition removal, pairs had resorted themselves significantly more in the misassorted group than in the assorted group (Table IV), with the most frequent outcome being that the large male pair-bonded with the large female monopolized the breeding site(s) (chi-square test: $X^2_4 = 67.85$, $P<0.001$). Table V summarizes the outcomes for both assortment groups. In four of the assorted and in one of the misassorted replicates, both pairs tolerated each other, each defending their initial pot on either side of the tank. Overall, large males dominated over small males significantly more than vice versa (59/72 replicates; chi-square test: $X^2_1 = 16.4$; $P<0.0001$), and this was true for both the misassorted and the assorted group (Table VI). Overall, large females dominated over small females significantly more than vice versa (48/72 replicates; chi-square test: $X^2_1 = 4.11$; $P<0.05$). Large female dominance over the small female was also significant in the assorted group but not in the misassorted group (Table VI).

Clutches were spawned by the dominant pairs in all of the 22 replicates left after the experiment was terminated. In the case of the single-pot treatment, all clutches were spawned in the pot by the dominant pair, whether there had been a switch (N=9) or the pair bond had remained intact (N=4). When there were 2 pots available, clutches were always laid in the initial pot of the dominant female, whether there had been a switch (N=5) or the pair bond had remained intact (N=4).

Mate removal experiment

Table VII describes the outcomes when one male or one female was removed in the misassorted replicates. The large male, when his mate was removed, was able to displace the small male and pair-bond with the female significantly more often than vice versa. The small male, when his female was removed, was never able to displace the large male and was chased by him. In contrast, the proportions of swiching were not significantly different when either male was removed and females interacted.

Regardless of which female's male was removed, both females performed frontal displays and mouthfighting to each other. The male was observed nipping and courting with both females and defending the pot, no matter which female he was paired with. Similarly, in either group of female removals, the female was observed nipping both males when these were mouthfighting. However, when the small male's large female was removed, the large male almost instantly chased the small male, intermittently courting with his female.

DISCUSSION

The data supported my main hypothesis that mate switching occurs when two pairs were misassorted with respect to mate quality (size). This can be explained, in part, by a preference for a higher-quality mate. Unlike in the assorted pairs where the large individuals restricted their courtship to each other and were aggressive primarily to individuals in the smaller pair, the large male, within the misassorted pair, equally courted with and chased both his own smaller female and the larger potential mate in the other pair, indicating an element of conflict presented by the availability of a better option. my finding that only the dominant pairs were observed to reproduce, regardless of whether intact or resorted, supports the better option hypothesis (Davies 1989, Ens et al. 1993), where only one of the divorcing partners should initiate and benefit from the change of mate. In contrast, the incompatibility hypothesis (Coulson 1972; Rowley 1983), where both divorcing partners should benefit from re-pairing with a more "compatible" mate, is not supported (however, see discussion on incompatibility below).

Although the larger male in misassorted pairs typically courted with the larger potential mate in the other pair, only 46% of the misassorted pairs eventually showed mate switching. In the remaining pairs, mate switching may have been prevented by a dominance relationship between females. Noonan (1983) and Haley (1987) demonstrated that, prior to pair formation, larger individuals typically defeat smaller ones in intrasexual competition. I found that although dominance for males is determined by size even after pair formation, female dominance is somehow affected by the size of her mate. When initially assorted, larger females defeated smaller females significantly more often than vice versa. However, in the misassorted group, where the smaller female was initially paired with the larger male, the larger female dominated only 59% of the time (NS). This finding indicates that a small female, being paired to a larger male, improves her chances of winning an aggressive encounter with a larger female. Mate switching and re-pairing of high-quality individuals ensued when both large males and females were able to displace the smaller consexual through combat. Resortment was prevented when smaller females defeated larger females in combat. The results of the preliminary mate removal experiment were consistent with the above data on intrasexual competition; that is, large males successfully displaced small males most of the time, whereas a large female was not always able to displace a smaller female paired with a high-quality male. Hence, divorce was dependent on the outcome of female competition. As female dominance was not dependent on relative size differences, other factors, such as the readiness to spawn, may be important.

The intruder presentations suggested that with increased size difference between pair members, the pair seemed less "compatible." That is, females much smaller than their mate spent more time hiding than females closer to their mate's size. When pairs were more size-matched, females performed more nips to their mate, thus seemingly less intimidated by the male. Previous studies also have suggested that females more similar to the male's size inhibited the male's aggression (Bastock 1967; Barlow 1977; Turner et al. 1989; Itzkowitz & Draud 1992). Furthermore, Baerends (1986) argued that individuals must reduce their aggressive drive to form pairs. Quite possibly, the pairs with the largest male/female size difference in the misassorted replicates where mate switching occurred were unable to form stable pair bonds with their initial mates.

Reducing the number of nesting sites from two to one did not influence mate switching suggesting that factors that increase the competition between pairs did not influence the likelihood of mate switching. It remains possible, however, that pairs were competing for breeding space, rather than nesting sites. As space was constant in all experiments, this aspect needs to be investigated further.

In summary, this is the first mate switching experiment in any monogamous species that varied mate quality while controlling for the confounding influence of past reproductive success. After pair-bond formation, large males defeated small males in aggressive encounters. These large males courted with and chased females equally only when their initial partner was a lower-quality mate but neglected and even rejected another female when their initial partner was a higher-quality mate, indicating a preference of these males for larger females. However, high-quality females were not always able to displace lower-quality females paired with higher-quality males and thus could not pair with them, even though they preferred these males. The mechanism by which small females paired with larger males acquired dominance over large females was not discernible from my experiment, but perhaps initial compatibility between male and female in a pair contributed to the stability of a pair bond.

Table I. Medians (ranges in parentheses) of variables monitored during the presentation of a small male intruder as a function of the size difference between male and female in a pair

		Male/female size difference				
		Similar size[a]	Intermediate[b]	Large[c]	H_2 [d]	P value
Time attacking intruder (s)	By male alone	104 (12-424)	42 (0-492)	61 (0-286)	2.46	0.29
	By female alone	123 (22-391)	89 (16-396)	73 (0-385)	2.06	0.36
	By pair together	167.5 (63-430)	91 (69-553)	90 (63-514)	5.00	0.082
Courtship frequency		29.5 (2-75)	15 (3-90)	12 (3-80)	1.50	0.47
Pot occupancy time (s)	By male alone	97 (0-384)	160.5 (0-560)	124 (0-471)	1.93	0.38
	By female alone	37.5 (0-226)	30 (0-465)	6 (0-459)	1.04	0.59
	By pair together	0 (0-302)	10.5 (0-421)	13 (0-516)	2.04	0.36
Aggression frequency	Male nips to female	0 (0-3)	0 (0-24)	0 (0-31)	4.79	0.091
	Female nips to male	0 (0-26)	0 (0-5)	0 (0-4)	6.13	0.042

[a] 0-0.9 cm difference, N=16; [b] 1.0-1.9 cm difference, N=32; [c] 2.0-3.5 cm difference, N=27; [d] Kruskal-Wallis ANOVA (H_2).

Table II. Medians (ranges in parentheses) of variables monitored when two pairs were competing over one and two breeding sites

		Number of breeding sites					
		One[b]		Two[c]		T[a]	P value
Intrasexual aggression time (s)	Between males	105.5	(5-860)	63	(24-476)	168	0.51
	Between females	127.5	(10-900)	128	(2-404)	170	0.58
Intersexual aggression time (s)	Large male/small female	3.5	(0-50)	27	(0-161)	213	0.15
	Large male/large female	7	(0-113)	0	(0-57)	170	0.58
	Small male/small female	0	(0-48)	0	(0-54)	196	0.53
	Small male/large female	0	(0-194)	15	(0-140)	204	0.30
Pot occupancy time (s)	Large male	101	(31-830)	99.5	(35-365)	165	0.90
	Small male	0.5	(0-868)	70	(0-352)	182	0.32
	Large female	0	(0-830)	50	(0-465)	149	0.50
	Small female	131	(0-860)	60.5	(0-534)	184	0.27
Courtship frequency	Large male/small female	0	(0-29)	2	(0-30)	190	0.73
	Large male/large female	8	(0-28)	11	(0-46)	176	0.77
	Small male/small female	0	(0-3)	0	(0-15)	225	0.071
	Small male/large female	0	(0-4)	0	(0-1)	180	0.92

[a] Mann-Whitney rank sum test (T), [b] N=25, [c] N=17.

Table III. Medians (ranges in parentheses) of variables monitored when groups of two pairs were initially misassorted and assorted

		Assortment group					
		Misassorted [b]		Assorted [c]		T [a]	P value
Intrasexual aggression time (s)	Between males	110	(5-860)	64	(24-476)	196	0.53
	Between females	115	(10-900)	132.5	(2-868)	193	0.61
Intersexual aggression time (s)	Large male/small female	0	(0-38)	37.5	(0-161)	136	0.027
	Large male/large female	28	(0-113)	0	(0-23)	223	0.049
	Small male/small female	4	(0-54)	0	(0-20)	163	0.37
	Small male/large female	0	(0-53)	35	(0-194)	133	0.019
Pot occupancy time (s)	Large male	84	(31-830)	101	(31-533)	192	0.43
	Small male	46	(0-700)	7	(0-868)	186	0.61
	Large female	0	(0-830)	9	(0-465)	207	0.11
	Small female	20	(0-559)	149	(0-860)	164	0.57
Courtship frequency	Large male/small female	7	(0-30)	0	(0-6)	243	0.0032
	Large male/large female	2	(0-35)	16	(0-46)	130	0.012
	Small male/small female	0	(0-1)	0	(0-15)	163	0.366
	Small male/large female	0	(0-4)	0	(0-1)	195	0.56

[a] Mann-Whitney rank sum test (T), [b] N=22, [c] N=20.

Table IV. Frequencies of resortment (switching) when groups of two pairs were initially misassorted and assorted

Assortment group	Switch	No Switch
Misassorted [a]	23	23
Assorted [b]	6	20

Chi-squared test: $X^2_1 = 5.01$, $P<0.03$

[a] N=46

[b] N=26

Table V. Dominant pairs after competition when groups of two pairs were initially misassorted and assorted

Assortment group	Resorted dominant pairs	Frequency	Intact dominant pairs	Frequency
Misassorted[a]	Large pair	21	Large male, small female	14
	Small pair	1	Small male, large female	6
	Pair tolerance	1	Pair tolerance	3
Assorted[b]	Large male, small female	5	Large pair	19
	Small male, large female	1	Pair tolerance	1

[a] N=46

[b] N=26

Table VI. Large male and female dominance over smaller consexuals in the misassorted and assorted groups

Assortment group		Percentage	X^2_1	P value
Misassorted [a]	Large male dominant	76.09%	6.72	<0.01
	Large female dominant	58.70%	0.70	NS
Assorted [b]	Large male dominant	92.31%	11.3	<0.001
	Large female dominant	76.92%	4.06	<0.05

Percentages of cases where the larger male was dominant over the smaller male and where the larger female was dominant over the smaller female. P values for chi-squared test (X^2_1) indicate whether the outcome percentages are significantly different from random.

[a] N=46

[b] N=26

Table VII. Frequencies of resortment when either a male or a female was removed from one of two pairs competing over a single breeding site

Removal	Remaining pair and solitary individual	Switch	No switch	P value
Female	Female/Small male and Large male [a]	5	1	0.008*
	Female/Large male and Small male [a]	0	6	
Male	Male/Small female and Large female [a]	2	4	0.455
	Male/Large female and Small female [b]	1	4	

All replicates were initially set up as misassorted, and a different individual was removed in each of the four groups prior to partition removal. An intact pair was then exposed to the remaining individual whose mate had been removed. P values are for Fisher's exact test.

[a] N=6

[b] N=5

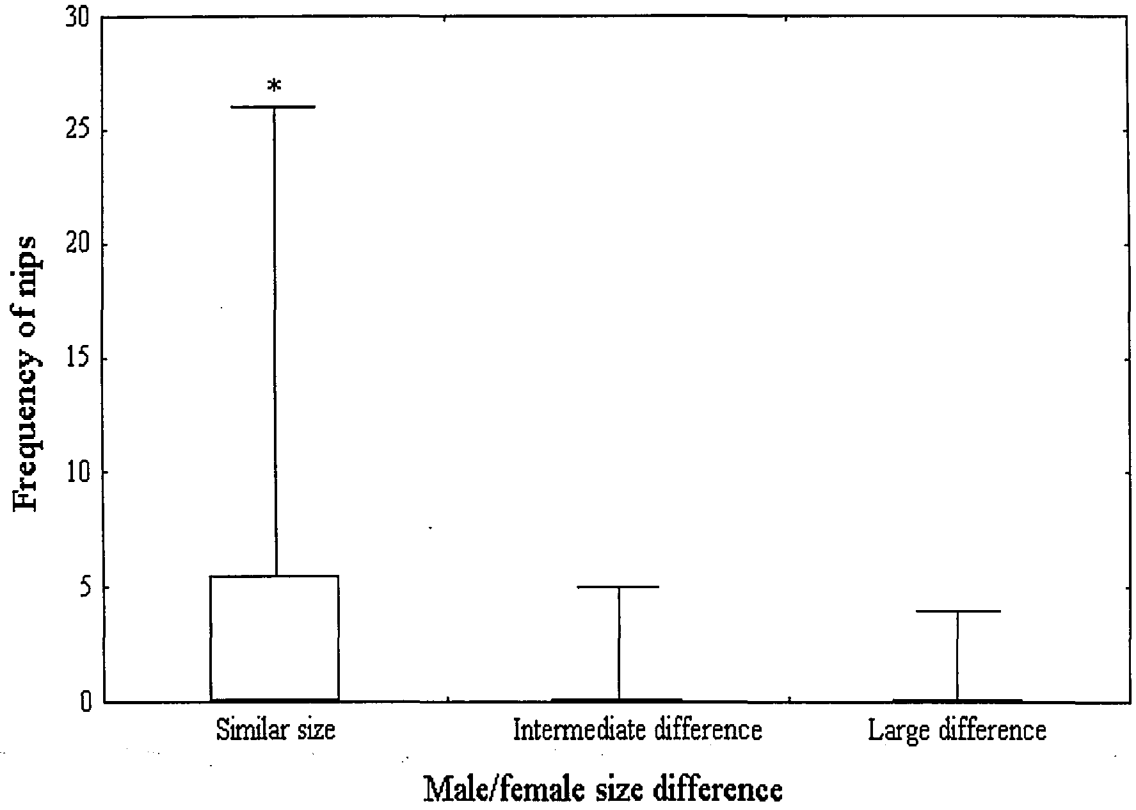

Figure 1.

Median number of nips females performed to males when paired individuals were similar in size (N=16), intermediately different (N=32) and largely different in size (N=27). Asterisk indicates which group differs significantly from the others (Dunn's test: $P<0.05$).

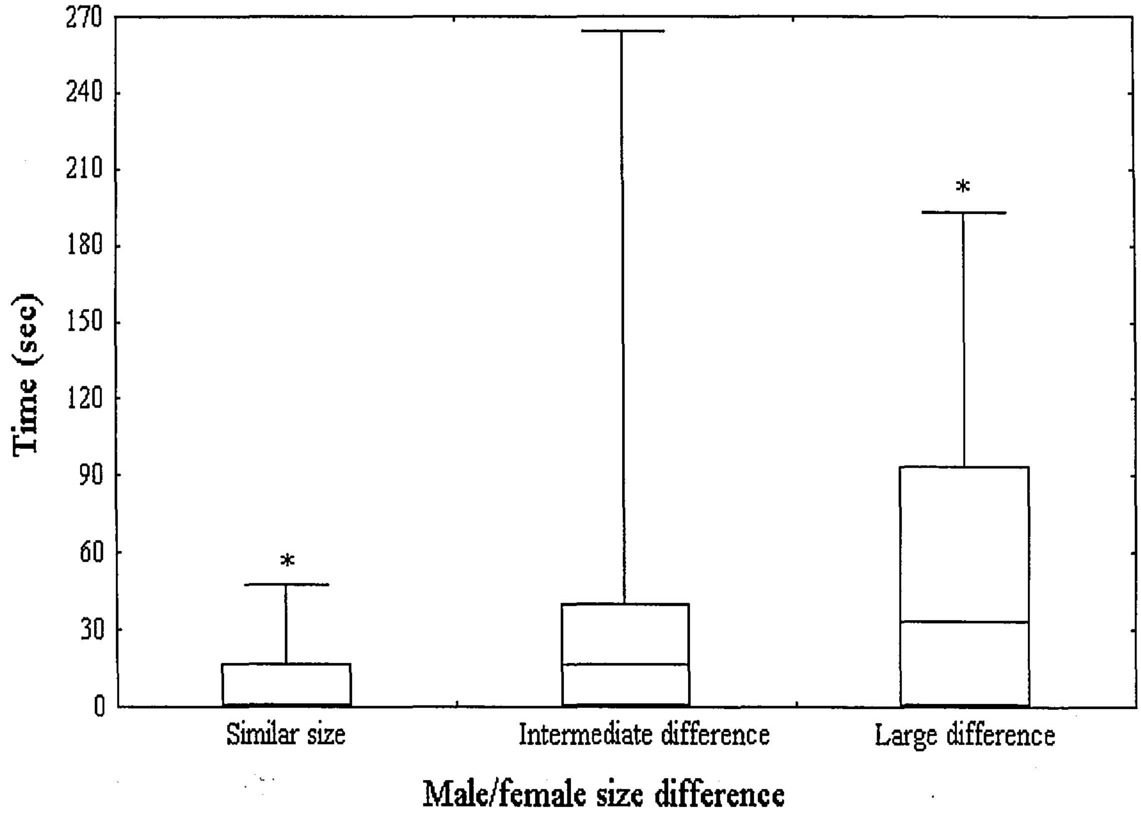

Figure 2.

Median time females spent hiding when paired individuals were similar in size (N=16), intermediately different (N=32) and largely different in size (N=27); Kruskal-Wallis test: $H_2=6.13$, $P<0.05$. Asterisks indicate which groups differ significantly from one another (Dunn's test: $P<0.05$).

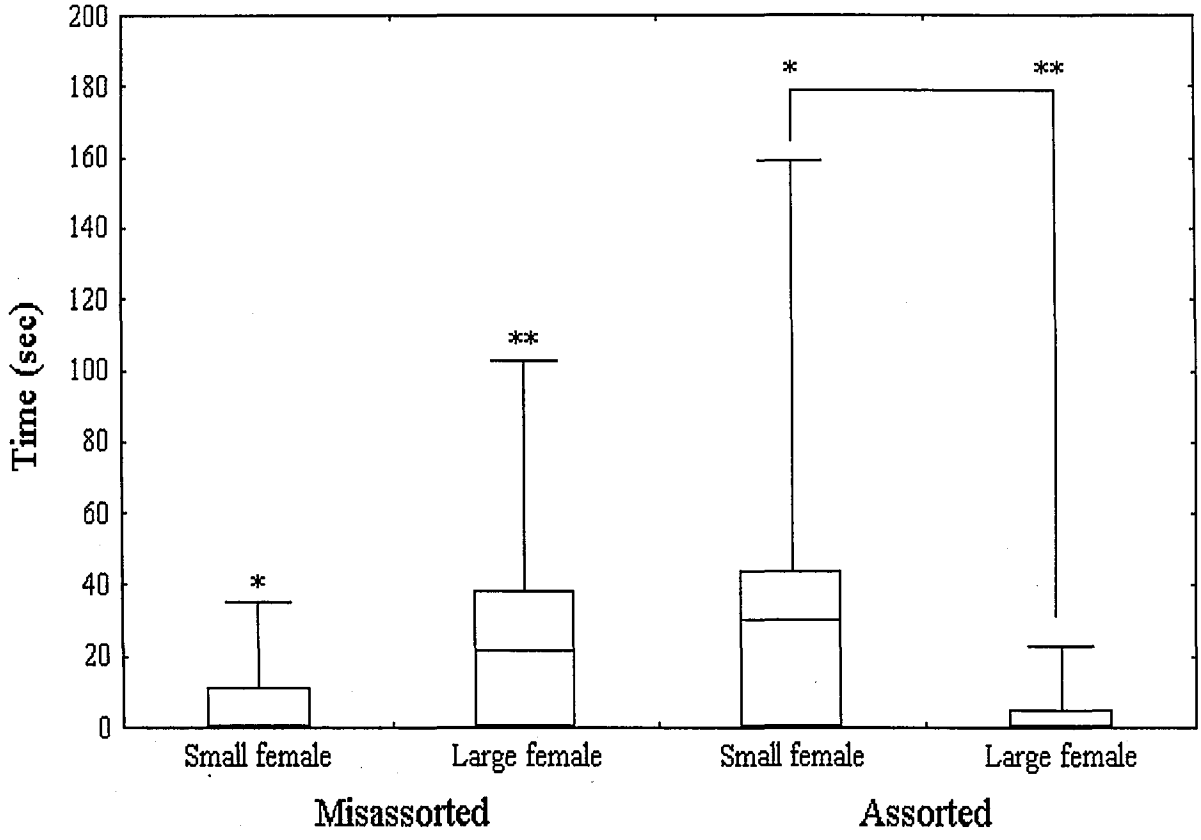

Figure 3.

Median time large males chased small and large females in the misassorted (N=22) and the assorted (N=20) group; similar asterisks and line indicate which two variables differ significantly.

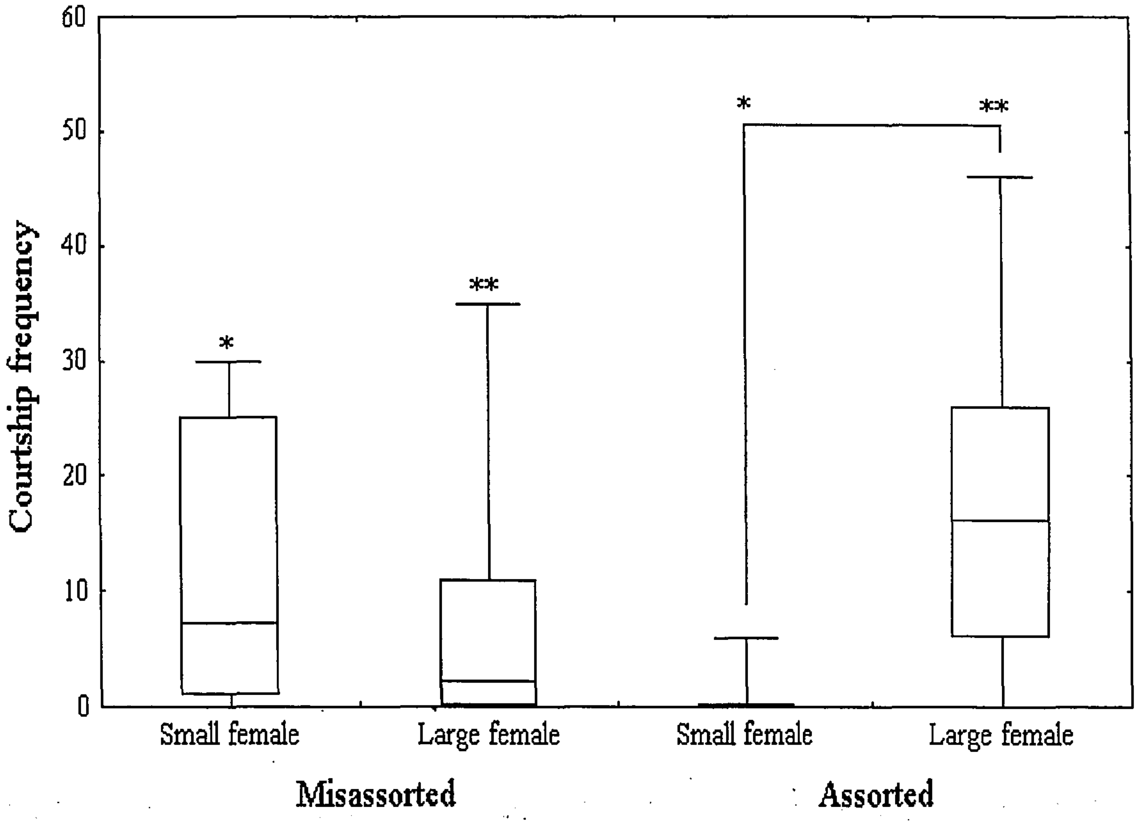

Figure 4.

Median frequency of courtship between large males and small and large females in the misassorted (N=22) and the assorted (N=20) group; similar asterisks and line indicate which two variables differ significantly.

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VITA

I was born in Frankfurt, West Germany (at the time), on June 21, 1972, to Karin and Axel Triefenbach. In 1978, I attended Frankfurt International School, where I was to enjoy a diverse education for the next 12 years. I developed an interest in biology during my senior year in high school, having focused mainly on artistic endeavors until then. This dichotomy of interests continued when I attended Lehigh University in 1990. After I graduated with my BSc in Biology/ Music in 1994, I continued in the Master's program in Behavioral and Evolutionary Biosciences. During my 3 years in Graduate School, I have taught numerous laboratories/ recitations in various fields, including Molecular Biology, Animal Behavior, Behavioral Neuroscience and Neuroanatomy of Behavior, in addition to conducting research. The findings in this thesis were the most striking of my brief career so far, and have been submitted for publication. Other research experience includes work on adult aggression vs. juveniles in *Stegastes leucosticus* and *S. planifrons* in Discovery Bay, Jamaica, and division of labor during courtship and parental care in *Cichlasoma nigrofasciatum.*

END

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