Behav Ecol Sociobiol (2001) 51:8–16
DOI 10.1007/s002650100411

ORIGINAL ARTICLE

Kazue Asoh · Tomoko Yoshikawa

Female nest defense in a coral-reef fish, *Dascyllus albisella*, with uniparental male care

Received: 31 October 2000 / Revised: 21 June 2001 / Accepted: 29 July 2001 /

Abstract Intraspecific variation in the patterns of parental care has been observed in a variety of animals; however, the possibility of parental care by a non-caregiving parent of uniparental species has not been thoroughly explored. In the coral-reef damselfish, *Dascyllus albisella*, only males normally exhibit parental care. In this study, we examined the response of females of this species to egg predators after experimental male removal and an elevated level of egg predation, at two small patch reefs (reefs 1 and 2) in Hawaii. We tested theoretical expectations that a nest was defended only by females which had spawned in the nest, and that larger females had a higher likelihood of defense than smaller females. A nest was defended against egg predators more frequently by females that had spawned in that nest than would be expected by chance. Not all females that had spawned in a given nest participated in defense. There was a positive association between female body length and the likelihood of defense at reef 2, but not at reef 1. Within a set of females that had spawned in the same nest during the same nesting cycle, defending females had larger body lengths than non-defending females at reef 2 but not at reef 1. Lack of association between female size and likelihood of defense at reef 1 was unexpected, but may correlate with the smaller average female size and smaller size differences among females on that reef.

Keywords Uniparental male care · Male removal · Elevated predation level · Female nest defense · Damselfish

Communicated by J. Krause

K. Asoh (✉) · T. Yoshikawa
Department of Zoology and Hawaii Institute of Marine Biology,
University of Hawaii, 2538 The Mall, Honolulu, HI 96822, USA
e-mail: asoh.1@osu.edu
Tel.: +1-614-292-1613, Fax: +11-614-292-0181

Present address:
K. Asoh, Aquatic Ecology Laboratory, Department of Evolution,
Ecology, and Organismal Biology, The Ohio State University,
1314 Kinnear Rd., Columbus, OH 43212-1156, USA

Introduction

Intraspecific variation in the patterns of parental care has been observed in a variety of animals (Clutton-Brock 1991; Gowaty 1996). The variation is mainly observed in the number of caregiving parents, but is also seen in the sex of a caregiver, as well as, in biparental species, in the amount of care provided by one parent in response to its mate's contribution.

The questions as to whether or not parents should provide care and which of the two parents should provide care have been discussed using game theoretical models of parental care (Maynard Smith 1977, 1982; Grafen and Sibly 1978; Vehrencamp and Bradbury 1984). Incorporating parameters that affect costs and benefits of care by male and female parents, these models specify conditions under which different patterns of parental care are favored.

The basic model by Maynard Smith (1982) incorporates three sets of parameters: probability of offspring survival with no care, uni- and biparental care, a male's chance of remating with and without his providing care for his offspring from the first mating, and the number of eggs laid by a female with and without her providing care for her offspring from the first mating. Various ecological factors, such as spatial and temporal dispersion of resources and mates, abundance of resources, and degree of predation on guarding parents or offspring, influence the values of these parameters. A difference in the parameter values between populations of a single species, or a difference in the parameter values in a single population between years is predicted to lead to intraspecific variation. Shifts in the parameter values accompanying offspring growth are expected to lead to a shift in the pattern of care in a single pair during offspring development.

Many empirical studies conform to the overall predictions of the model. In some bird and fish species, a shift in operational sex ratio toward female bias, together with an increased level of food resource or a decreased level of predation (and thus a shift in the probability of offspring survival with uni- and biparental care, and males' chance of remating), often results in a shift from bi- to uniparental female care (Clutton-Brock 1991; Keenleyside 1991). In several cichlid fishes which care for offspring until the fry stage, a difference in the probabilities of offspring survival between either eggs or wriggler and fry results in a shift from uniparental care by either parent to biparental care (Kuwamura 1996).

Facultative alteration of parental care by one parent in response to its mate's contribution in biparental species has been modeled as an evolutionarily stable and optimal investment strategy (Chase 1980; Houston and Davies 1985; Winkler 1987; Kacelink and Cuthill 1990). The models focus on a “bargaining” process between male and female parents of monogamous biparental species, in which each member of a pair adjusts its expenditure according to that of its mate, eventually reaching an equilibrium. The models predict that, except when a parent is constrained to very low levels of parental expenditure, the optimal response to a reduction in expenditure by a partner is for the other to increase its own expenditure, but by a smaller amount, insufficient to compensate for the reduction by its partner.

Support for the predictions comes from “handicapping” and mate removal studies in primarily monogamous avian species in which both parents usually participate in feeding the young (Clutton-Brock 1991; Gowaty 1996). When either the male or female parent of a pair is handicapped by attaching small weights to its tail, it decreases the rate of food delivery (handicapping on both sexes: Wright and Cuthill 1989, 1990; handicapping on female: Markman et al. 1995). The unhandicapped parent increases its rate of food delivery, even though its compensatory increase is incomplete. Increased rates of food delivery by a parent in response to experimental mate removal have been reported for many other bird species. In some species, the remaining parent only partially compensates for the lack of its mate (male removal: Alatalo et al. 1982; Lyon et al. 1987; Wolf et al. 1990; Meek and Robertson 1994; Markman et al. 1996; both male and female removals: Leffelaar and Robertson 1986), but almost fully compensates by making as many food deliveries as a pair working together in other species (male removal: Weatherhead 1979; Smith et al. 1982; Whillans and Falls 1990; Duckworth 1992; Dunn and Hannon 1992). Males and females of biparental cichlid fishes also alter their parental behavior when their mates are removed (Mrowka 1982; Lavery and Reebs 1994).

Uniparental care is widely distributed among vertebrate classes (Clutton-Brock 1991; Gowaty 1996). What should a non-caregiving parent of uniparental species do when a condition that necessitates care by both parents for offspring survival arises? What should a non-caregiving parent do when its mate, which normally is the sole provider of the care, disappears or dies? These questions have not been thoroughly explored. The lack of studies might have resulted from our assumption that a parent that does not normally participate in parental care is not capable of doing so. But is this assumption always reasonable? The ecological factors that affect the costs and benefits of care by male and female parents is likely to differ spatially and temporally. The disappearance or death of a single caregiving parent is a phenomenon that occurs in nature. Non-caregiving parents ought to assume the parental duty if the benefits of caring gained through increased survival of the current offspring outweigh its costs, such as increased mortality, decreased future fecundity, or decreased future mating opportunities. When conditions that give a selective advantage to those parents who provide care occur repeatedly throughout a population, natural selection would favor a proximate mechanism that allows assumption of parental duty under these conditions.

The Hawaiian dascyllus, *Dascyllus albisella*, is a coral-reef damselfish (family Pomacentridae) that exhibits uniparental male care (Stevenson 1963; Barash 1980; Danilowicz 1995a, 1995b; Godwin 1995). Uniparental male care is the predominant form of care in the damselfish family Pomacentridae (Thresher 1984). Of approximately 300 species in 28 genera in four subfamilies, biparental care is known to be restricted to the subfamily Amphiprioninae (28 species) and 1 genus *Acanthochromis* in the subfamily Chrominae (1 species), both of which also exhibit a monogamous mating system (Thresher 1984; Allen 1991; Nelson 1994). Our preliminary findings in *D. albisella*, however, indicated that a nest was jointly defended against egg predators by the male parent and its female mates under an elevated level of egg predation (Asoh 2001), and that a nest was defended by female parents when the nest-guarding male was removed using a blocking net.

In this study, we expanded our investigation and examined the status of defending females. Nest defense is adaptive only when the benefits of defense outweigh its costs. There is little benefit to a female which defends nests that do not contain her eggs. We first tested a theoretical expectation that a nest was defended only by females that had spawned in that nest. We tested this expectation against two alternative hypotheses that propose a less precise relationship between spawning and defense. The first alternative hypothesis (Ha1) stated that any female whose home range included the nest in question would provide defense. The second alternative hypothesis (Ha2) stated that any female who had spawned anywhere during the current nesting cycle and whose home range encompassed the nest in question would provide defense.

We then tested whether females of larger body sizes had a higher likelihood of defense than smaller females. Body size is an important life history character that is often correlated positively with competitive ability to acquire resources and ability to deter offspring predators, and negatively with the risk of injury or death from predation. Larger females may be better at acquiring food, and hence can invest more energy in absolute terms in defense (Clutton-Brock 1984). Larger females should be more intimidating and thus more effective in deterring potential egg predators (Keenleyside et al. 1985). Larger females may also experience a lower risk of injury or death from predation during defense. The reduction in future reproductive success due to defense, through decreased survival, growth, and future fecundity, may also be smaller for larger individuals (Clutton-Brock 1991). Larger females are thus expected to have higher overall benefits of defense, and hence to show a higher likelihood of defense than smaller females.

Methods

Study species

The study species, *D. albisella*, is a planktivorous damselfish endemic to the Hawaiian Islands and Johnston Atoll (Randall and Allen 1977). Juveniles are associated with small coral heads, whereas adults form feeding aggregations over the reefs (Stevenson 1963; Booth 1991, 1992). In Hawaii, spawning occurs throughout the year with the peak from June to September or October (Stevenson 1963; Danilowicz 1995a). During the peak, spawning is highly synchronous within local populations and occurs every 5–7 days (Danilowicz 1995b). Prior to spawning, males prepare completely open nests by removing sand, silt, and other debris from an area of the reef substratum, such as dead portions of coral surfaces, the upper surfaces of dead coral rubble buried in sand, or rock surfaces (Stevenson 1963; Asoh 2001). On the day of spawning, females travel to a male's nest and lay demersal eggs (Stevenson 1963). After spawning, females leave the nest and join feeding aggregations (Stevenson 1963). The mating system is polygynandrous (personal observations). Females generally mate with only one male per nesting cycle (Asoh 2001), but with different males over multiple nesting cycles (personal observations). Males generally mate with more than one female per nesting cycle (Stevenson 1963). Eggs are tended and guarded by male parents until hatching, which occurs at dusk on the 4th day after spawning at temperatures ranging from 26.2 to 28.9°C (Stevenson 1963; Danilowicz 1995a).

Spawning-data collection

We conducted this study using SCUBA from 29 August to 22 September 1998 on two small patch reefs (designated as reefs 1 and 2) located in the Sampan channel, Kaneohe Bay, Oahu, Hawaii. Reefs 1 and 2 measured 10×8 m^2 and 2×2 m^2, respectively, and were separated from each other by a distance of 40 m. The reefs were 2–3 m deep, and were surrounded by a bare sandy bottom. Prior to the start of the study, we censused the two reefs and marked the positions of male nests. We then collected fish, measured them to the nearest 0.5 mm standard length (SL), sexed them by the shape of the urogenital papilla, and marked them by injecting elastomer dye under the scales (Northwest Marine Technology). We marked a total of 30 out of 35 nesting males and 98 females at reef 1, and a total of 20 out of 24 nesting males and 60 females at reef 2. We distinguished nine individual unmarked nesting males by natural differences in scale pattern and scar marks (see Danilowicz 1995b). During this study, spawning occurred every 5–7 days on both reef 1 and reef 2, with all spawning on a reef concluded within 2 days. Fish spawned 1–2 days later on reef 2. On the spawning days for each reef, we censused all the nests on the reef every 15–45 min, depending on the number of active nests (defined as nests with females in the act of spawning or waiting their turn to spawn). We recorded the identities of nesting males, identities of their female mates, and whether the females were in the act of spawning or waiting. A single female generally spent 2–4 h for egg laying (Asoh 2001), and censusing the nests with 15- 45-min intervals allowed us to obtain almost a complete record on which female spawned with which male. We began the census at 0600 hours and continued until no active nests were found on the reef for 1 h (generally 1600–1800 hours).

Of all females that were observed to spawn in each nesting cycle, 81.3±7.8% (mean±SD, *n*=4 nesting cycles) were marked females at reef 1, and 82.1±8.3% (*n*=4 nesting cycles) at reef 2.

Field manipulation

Our preliminary findings indicated that either an elevated level of predation, male absence, or a combination of both would elicit nest defense in female parents. To give females a maximum stimulus for nest defense, we removed nesting males from their nests and placed overturned rocks around the nests to attract egg predators. At the onset of each experimental manipulation, females were in the feeding schools in the water column, and no *D. albisella* individuals except the guarding male was present at each nest. We recorded the identities of females that descended from the feeding schools to defend the nests within 10 min of male removal. A female was scored as defending a nest when she chased a major egg predator, either the saddle wrasse, *Thalassoma duperrey* or conspecific *D. albisella*, within a radius of approximately 1 m from the nest. Such behavior was never observed outside the context of nest defense. The nests were covered with a nylon mesh to prevent egg loss from predation during experiments. The nesting males were returned to their nests at the end of each 10-min trial. We conducted a total of 70 trials (45 at reef 1 and 25 at reef 2) during four nesting cycles. In each nesting cycle, experimental nests were randomly chosen from the nests that obtained eggs during that cycle. Trials were made on various days during the 4-day incubation period (42 on day 1, 26 on day 2, 0 on day 3, and 2 on day 4). We performed more trials early in the incubation period because eggs at the earlier stages attracted more egg predators (personal observations). On spawning days, trials were conducted at least 1 h after the cessation of all spawning activity on the reefs. The average nearest-neighbor distance of nests measured 1 year prior to this study was 1.14±0.39 m (*n*=31) at reef 1 and 1.63±0.85 m (*n*=24) at reef 2.

Who defends nests?

We counted the number of nests in two categories: a nest of the first category was defended only by females that were observed to spawn in that nest (spawned females). A nest of the second category was defended by at least one female that was not observed to spawn in that nest (non-spawned females), regardless of whether spawned females defended or not. We calculated, for each nest and in each male removal, the expected probability of that nest being defended only by spawned females (P_s), and the expected probability of that nest being defended by at least one non-spawned female (P_n) by the following equations:

$$
\begin{aligned}
P_s &= \sum_{k=1}^{N_s} \frac{N_s(N_s-1)\cdots(N_s-k+1)}{N_t(N_t-1)\cdots(N_t-k+1)} \\
&= \frac{N_s}{N_t} + \frac{N_s(N_s-1)}{N_t(N_t-1)} + \cdots + \frac{N_s(N_s-1)\cdots(N_s-k+1)}{N_t(N_t-1)\cdots(N_t-k+1)} \\
&\quad + \cdots + \frac{N_s(N_s-1)\cdots 1}{N_t(N_t-1)\cdots(N_t-N_s+1)} \\
P_n &= 1 - P_s
\end{aligned}
$$

N_s was the number of marked females observed to have spawned in that particular nest. In evaluation of the hypothesis that any female whose home range included the nest would provide defense (Ha1), N_t was the total number of marked females whose home range encompassed that nest. At each reef, females moved about in an area that was even larger than the reef (K. Asoh, T. Yoshikawa and G.S. Losey, unpublished data). In other words, their home ranges encompassed all the nests on their resident reef. Therefore, N_t is equivalent to the total number of females originally marked at each reef. In evaluation of the hypothesis that any female who had spawned during the current nesting cycle and whose home range encompassed the nest would provide defense (Ha2), N_t was a the total number of marked females who had spawned in the current nesting cycle and whose home range encompassed that nest. The *k*th term in the first equation represents the probability of a nest defended by *k* spawned females.

To obtain expected frequencies of the two categories (F_s and F_n), we added probabilities of all of the nests in each category (i.e., $F_s = \Sigma P_s$, and $F_n = \Sigma P_n$). We compared the observed and expected frequencies using the *G*-test (likelihood ratio test) with William's correction. Some nests failed to attract egg predators, and some were defended by males of the adjacent territories and no female came to defend them. These two types of nests were excluded from the analyses. Unmarked females were also excluded from the analyses.

Likelihood of defense by females of different body size

To determine whether larger females had a higher likelihood of defense than smaller females, we classified females that had spawned in nests defended by at least one female into two classes of different defending tendencies: a defender who participated in nest defense at least once, and a non-defender who never participated in defense. We performed Mann-Whitney *U*-tests (one-tailed) to determine whether defender length (SL, mm) exceeded non-defender length.

We also tested whether larger females had a higher likelihood of defense than smaller females within a group of females that had spawned in the same nest during the same nesting cycle (potential defenders). In 23 removals at reef 1 and 18 removals at reef 2, a set of females that spawned in the same nest during the same nesting cycle included both defenders and non-defenders. We developed a randomization test (Appendix 1) to determine whether defender length exceeded non-defender length within sets of potential defenders more often than would be expected by chance.

Because the results from reefs 1 and 2 differed, comparing the difference in length distribution between the two reefs and examining how the inter-reef difference in length distribution was reflected in the difference in length among potential defenders became necessary. We used length data from a total of 48 marked females at reef 1 and a total of 33 marked females at reef 2 that had spawned in the nests defended by at least one female. We performed the Mann-Whitney *U*-test (two-tailed) to determine whether the size distribution of female lengths differed systematically between the two reefs. We also compared the length difference among potential defenders between the two reefs. We used data from 23 removals at reef 1 and 18 removals at reef 2 that elicited female nest defense and where more than one female had spawned. A randomization test (Appendix 2) was developed to determine whether mean length difference between females of consecutive size ranks within the potential defenders differed between the two reefs.

Results

The experimental nest was defended by at least one marked female in 50 out of 70 removals. In the remaining cases, the nest was defended by a neighboring nesting male(s) (*n*=8), by an unmarked individual(s) (*n*=4), or defended by none (*n*=8). The number of defending marked females ranged from one to three (one defender *n*=32, two defenders *n*=17, three defenders *n*=1). None of the defending females ate eggs in the nests or picked on the surfaces of the overturned rocks. Of the cumulative 69 female defenders, 60 (87%) were observed to have spawned in the nests they defended.

Table 1 Observed and expected frequencies of nests defended only by spawned females and by at least one non-spawned female based on two alternative hypotheses. The first alternative hypothesis (*Ha1*) stated that any female whose home range included the nest in question would provide defense. The second alternative hypothesis (*Ha2*) stated that any female who had spawned anywhere during the current nesting cycle and whose home range encompassed the nest in question would provide defense.

Reef	Frequency		Spawned defense	Non-spawned defense
1	Observed		21	8
	Expected	Ha1	0.91	28.09
		Ha2	2.27	26.73
2	Observed		20	1
	Expected	Ha1	1.08	19.92
		Ha2	2.46	18.54

Who defends nests?

Females that engaged in the defense of experimental nests were not a random sample of females in the immediate area. The hypothesis of a nest being defended by any female whose home range encompassed that nest (Ha1) was rejected with a very high level of significance at both reefs (Table 1; *G*-test: *G*=109.8, *P*<0.001 at reef 1; G=108.3, *P*<0.001 at reef 2). The hypothesis of a nest being defended by any female whose home range encompassed the nest in question when she had spawned during the current nesting cycle (Ha2) was also rejected with a very high level of significance (Table 1; *G*-test: *G*=72.8, *P*<0.001 at reef 1; *G*=76.2, *P*<0.001 at reef 2). Eight nests at reef 1 and one nest at reef 2 were defended by at least one non-spawned female. These females were not observed to spawn in the nests in question nor observed to spawn in any nests on their resident reefs.

Likelihood of defense by females of different body size

A total of 48 marked females at reef 1 and a total of 33 marked females at reef 2 spawned in the nests defended by at least one female. Defender length was significantly larger than non-defender length at reef 2 (Mann-Whitney *U*-test: *U*=206, N_1=18, N_2=15, one tailed *P*=0.005; Fig. 1), but not at reef 1 (Mann-Whitney *U*-test: *U*=298, N_1=27, N_2=21, one-tailed *P*=0.38; Fig. 1). Within a set of females that had spawned in the same nest during the same nesting cycle (potential defenders), defenders were significantly larger than non-defenders at reef 2 (randomization test: *P*=0.0001), but not at reef 1 (randomization test: *P*=0.70; Fig. 2).

The distribution of female lengths at reef 2 was more skewed than that at reef 1 with more fish in the larger size range than at reef 1 (Fig. 3a). The distribution differed systematically between the two reefs, and female length was larger at reef 2 than at reef 1 (Mann-Whitney *U*-test: *U*=1148, N_1=48, N_2=33, two-tailed *P*=0.0006).

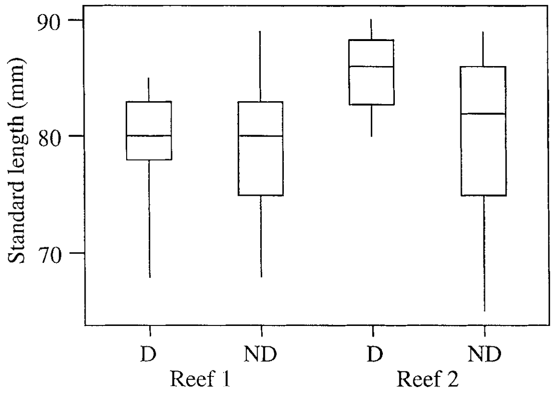

Fig. 1 Box plots of standard lengths of defenders (*D*) and non-defenders (*ND*) at reef 1 and reef 2. The *line drawn across each box* indicates the median. The *bottom and top edges of the box* indicate the first and the third quartiles, respectively. The *whiskers* extend to the minimum and maximum

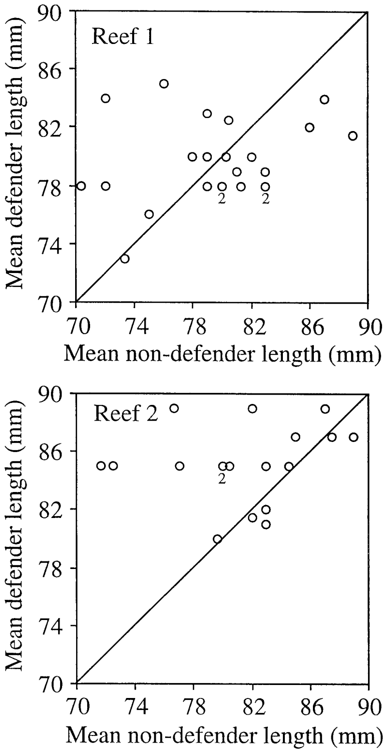

Fig. 2 Relationship between mean defender length and mean non-defender length within potential defenders at reef 1 and reef 2. *Diagonal lines* represent lines of no difference between the two variables. *Numbers* below circles indicate the number of overlapping data points

The distribution of mean length differences among potential defenders at reef 2 had a larger median and a wider spread than that at reef 1 (Fig. 3b). However, there was no statistically significant difference in mean length difference between the two reefs (randomization tests: *P*=0.56).

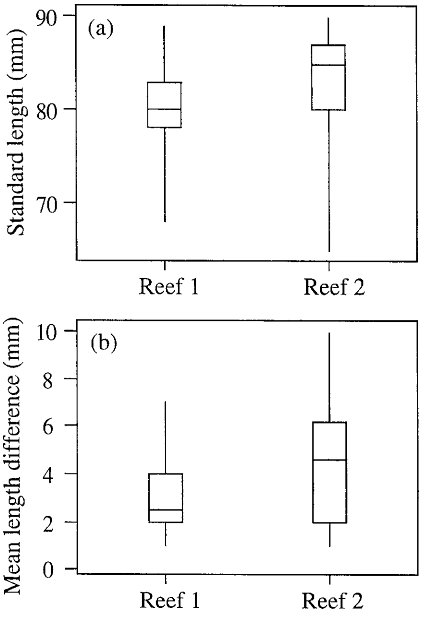

Fig. 3 Box plots of female standard lengths (**a**) and mean length differences (**b**) at the two reefs. The *line drawn across each box* indicates the median. The *bottom and top edges of the box* indicate the first and the third quartiles, respectively. The *whiskers* extend to the minimum and maximum

Discussion

Female nest defense

Female *D. albisella* defended nests against egg predators under the combined condition of the absence of the parental male and an elevated level of egg predation. A parent that did not normally participate in parental care was capable of providing at least some aspect of that care, showing that flexibility in parental care is not limited to parents of primarily monogamous biparental species.

One might argue that females came to defend the new food source on the overturned rocks or in the unattended nest. If this was the case, we would expect females engaged in defense to be a random sample of females in the immediate area; however, the experimental nests were defended more frequently by females that had spawned in that nest than would be expected by chance. This suggests that females came to defend their eggs in the nests rather than to defend the new food source. In addition, we observed none of the defending females picking on the surfaces of the overturned rocks or the eggs in the nest.

Occurrence of female nest defense in *D. albisella* is probably related to the intermediate nature of its social organization among damselfishes. To make defense effective, a female has to detect loss of her mate and potential egg predators around the nest quickly, and thus must be in the relative vicinity of the nest. *D. albisella* females are not territorial in our study site and stay in feeding aggregations. Females are, nonetheless, relatively close to male nests because males establish nests around feeding aggregations. This contrasts with the social organization of many other schooling planktivorous or herbivorous damselfishes. In many schooling planktivorous damselfishes, males establish temporary breeding territories prior to spawning. Females swim far away from nest sites after spawning and do not stay close to male nests (Thresher 1984). Detection of male loss and egg predators may not be as easy as in *D. albisella*. In herbivorous damselfishes, both males and females defend permanent feeding territories against intruders. Leaving territories for defense would result in a higher cost of defense for females of these species due to a loss of food resources within their territories during their absence (Kohda 1988).

As predicted, most of the female *D. albisella* that defended a nest were confirmed to have their eggs in that nest. In contrast to nest defense by neighboring males, which could be explained as an extension of defense of their own nests, avoidance of potential future predation risk to their own nests, or as a takeover of a neighboring territory, there is no benefit for a female to defend nests that do not contain her eggs, unless a defender is closely related to females that laid eggs in the nests. The pelagic larval stage of this species (Wellington and Victor 1989) makes such inclusive fitness effects unlikely. We employed a set of females as potential defenders with increasing conservativeness in the two alternative hypotheses. We incorporated proximity of females to nests to be defended in the first hypothesis, which stated that any female whose home range included the nest in question would provide defense. This criterion for potential defenders may be too loose because the motivational state of females for defense is likely to be primed by egg laying. We added this motivational factor in our second hypothesis, which stated that any female that had spawned during the current nesting cycle and whose home range encompassed the nest in question would provide defense. We showed that even with the more conservative alternative hypothesis, a nest was defended by females that had spawned in that nest significantly more frequently than random expectation. In addition, the few “non-spawned” defenders likely did spawn in the nests in question earlier in the day before we started our spawning observations. The nests defended by these “non-spawned” defenders already contained newly laid eggs at the start of our dawn observation. We did not see these defenders spawn in the nest in question, but we also did not see them spawn in any nest on their resident reefs.

The level of egg predation may vary temporally, and the death or disappearance of a sole caretaker is likely a normal part of an animal's life. An individual is expected to assume the parental duty if the benefits of caring gained through increased survival of the current offspring outweigh its costs, such as increased mortality, decreased feeding opportunities, decreased future fecundity, or decreased future mating opportunities, which can result from caring for offspring itself, as well as from maintaining vigilance over the caregiving mate and offspring. Nevertheless, we have found only a few studies showing that the non-caregiving sex was capable of performing some parental duties in species where only one sex provides care. This may partially be due to physiological limitations in the ability of each sex to carry out the role normally performed by its partner (Markman et al. 1996), especially in species where a sex-specific parental role requires special organs or structures, such as mammary glands and brood pouches.

Assumption of the parental duty by non-caregiving parents is perhaps more common among vertebrate groups, such as reptiles, amphibians, and fishes, in which the predominant form of care is guarding of offspring. The physiological cost of guarding is low compared to that for feeding the young (Regelman and Curio 1986; Markman et al. 1995), and thus is less likely to put the parent into physiological stress. It also does not require any special structures or organs. In accordance with this prediction, flexibility in the caretaker's sex in uniparental species has been reported for a few amphibian and fish species in which parental care mainly comprises egg guarding. In some terrestrially breeding frogs with direct development (Simon 1983; Townsend 1996; Bourne 1997) and an aquatic salamander (Durand and Vandel 1968), parental care is uniparental but is provided by either sex. In the filefish, *Rudarius ercodes*, care is predominantly maternal, but there are cases of biparental or paternal care (Kawase and Nakazono 1995).

In this study, we focused on the status of defending females. There are many questions unanswered. Is a combination of male absence and an elevated level of predation a necessary stimulus to elicit female defense? Can either one of these factors alone elicit female defense? Does a female provide other forms of care, such as fanning of eggs, which are normally provided by the male? Does a female defend the nest until hatching of the eggs? We can provide only partial answers to these questions. In this study, no female came to defend the nests when no predators were attracted to nests. This suggests that parental care by females is limited to the defense of nests against egg predators. No female came to defend the nests when the nests were defended by neighboring males. Furthermore, nine instances of joint defense against egg predators by the male parent and its female mates under an elevated level of egg predation have been seen in the field under natural conditions (Asoh 2001). This suggests that female defense is limited to a situation in which the amount of defense required is larger than the amount of defense provided solely by the guarding male. Finally, when a foreign male took over a nest after the disappearance of the resident male, the new male guarded the eggs till the day of hatching (personal observation). We hypothesize that the observed female nest defense is temporary and serves to protect eggs during a brief period of high predation or during a period between parental male disappearance and nest takeover by a new male.

Likelihood of defense by females of different size

The result from reef 2 agreed with our prediction that females of larger absolute size had a higher likelihood of defense. Within a group of females that had spawned in a nest, those of relatively larger size also had a higher likelihood of defense. It may be more adaptive for larger females to defend more frequently because they are more effective in defense, have a lower risk of injury or death from predation during defense, can afford more absolute energy for defense, or experience a smaller decrease in future reproductive success, and thus are expected to have a larger positive balance in the costs and benefits of defense (Clutton-Brock 1984, 1991; Keenleyside et al. 1985).

Lack of association between female size and the likelihood of defense at reef 1, a reef separated by only 40 m from reef 2, was unexpected. The distribution of female lengths differed between the two reefs and suggests that a slight difference in size distribution could lead to differences in behavior. Median female length was larger at reef 2 than at reef 1, and potential defenders tended to be of more similar sizes at reef 1 than at reef 2. Females of similar sizes are presumably of similar age and thus are expected to have similar residual reproductive success. When potential defenders are of similar sizes, factors unrelated to size, such as body condition, might become more important determinants of the adaptive value of defense. Proximate factors such as a failure to accurately assess relative sizes among a group of similarly sized females could also be a factor. The ultimate and proximate reasons for differences in defense behavior between the reefs, however, need further examination.

There are many other potential factors that could have increased the variability in our results. First, we were not able to control for the level of predation. Removal of nesting males and placing of overturned rocks attracted predators and hence induced nest defense in females, but the number of predators varied. For example, suppose that a female was the sole mate of a given male. She may have engaged in nest defense when the predation level was intermediate and the benefits of defense outweighed its costs. The same female may not have defended if the predation level was too high for a single individual to be a successful defender. Second, the number and the size distribution of potential defenders varied widely. If the mating system of *D. albisella* were monogamous, whether a female should engage in defense would be determined by the costs and benefits of her own defense. *D. albisella* males, however, generally mate with more than one female per nesting cycle. The costs and benefits of nest defense to a given female, then, are expected to be affected by the number and size of females that spawned on the same nest during the same nesting cycle and whether or not these other females defend. For example, suppose that a female was the sole mate of a given male in one case and one of the three mates in another. She may have engaged in nest defense in the former case but not in the latter because another female has already started defending the nest. A game-theoretical approach is necessary for deeper understanding of the dynamics of the female defense behavior observed, because whether a female should defend or not depends on what the other females are expected to do.

Acknowledgements We are deeply indebted to G.S. Losey for encouragement, constructive advice, computer programming, and review of the manuscript, to A. Taylor for advice on data analyses, and to J. Stimson for discussion and review of the manuscript. We are also very grateful to the referee, S. Reebs, the anonymous referee, and the associate editor for their careful and sincere reviews and constructive comments. Our thanks also go to G. Aeby, G.C. Fiedler, J.R. Godwin, M. Kasuya, R. Langston, J. Mahon, D.A. Mann, S. Montreevat, D. Pence, and L. Privitera. The research was approved by the Institutional Animal Care and Use Committee of the University of Hawaii. This study was supported by the Department of Zoology and Hawaii Institute of Marine Biology at the University of Hawaii, by the East-West Center Degree Fellowship, Hawaii Audubon Society Research Grant, Raney Award from the American Society of Ichthyologists and Herpetologists, Sigma Xi Grants-in-Aid of Research, and International Women's Fishing Association Scholarship to K.A., and by the East-West Center Degree Fellowship and the East-West Center Field Work Scholarship to T.Y.

Appendix 1

Randomization test procedures for comparison of defender and non-defender lengths within a group of potential defenders.

1. For each of *n* removals (*n*=23 for reef 1, *n*=18 for reef 2, and *n*=41 for both reefs combined), we calculated the difference between the mean of defender lengths and the mean of non-defender lengths. We then calculated the mean of the *n* differences, which we defined as observed mean difference.
2. We shuffled all the observed female lengths, and randomly assigned lengths to defenders and non-defenders. With each female having a randomly assigned length, we calculated the difference between the mean of defender lengths and the mean of non-defender lengths. We then obtained the mean of the *n* differences, which we defined as random mean difference.
3. We repeated step 2 10,000 times, and calculated the proportion of random mean differences that were larger than the observed mean difference.

Appendix 2

Randomization test procedure for comparison of length difference among potential defenders between the two study reefs.

1. For each of 23 removals at reef 1 and 18 at reef 2, we calculated the mean size difference between the females of consecutively ranked size. We then calculated the difference in the mean of the mean size differences between the two reefs, which we defined as observed mean difference.

2. We shuffled all the observed female lengths, and randomly assigned lengths to females. With each female having a randomly assigned length, we calculated the mean size difference between the females of consecutively ranked size. We then calculated the difference in the mean of the mean size differences between the two reefs, which we defined as random mean difference.
3. We repeated step 2 10,000 times, and calculated the proportion of random mean differences that were larger than the observed mean difference. We multiplied the proportion by two and obtained the two-sided *P*-value.

References

Alatalo RV, Lundberg A, Stahlbrandt K (1982) Why do pied flycatcher females mate with already-mated males? Anim Behav 30:585–593

Allen GR (1991) Damselfishes of the world. Aquarium Systems, Mentor, Ohio

Asoh K (2001) Non-functional protogyny and reproductive ecology of the Hawaiian dascyllus, *Dascyllus albisella* (Family: Pomacentridae). PhD thesis, University of Hawaii

Barash DP (1980) Predictive sociobiology: mate selection in damselfishes and brood defense among white-crowned sparrows. In: Barlow GW, Silberberg J (eds) Sociobiology: beyond nature/nurture? Westview, Boulder, Colo, pp 213–226

Booth DJ (1991) The effects of sampling frequency on estimates of recruitment of the domino damselfish *Dascyllus albisella* Gill. J Exp Mar Biol Ecol 145:149–159

Booth DJ (1992) Larval settlement patterns and preferences by domino damselfish *Dascyllus albisella* Gill. J Exp Mar Biol Ecol 155:85–104

Bourne GR (1997) Amphisexual parental behavior of a terrestrial breeding frog *Eleutherodactylus johnstonei* in Guyana. Behav Ecol 9:1–7

Chase ID (1980) Cooperative and noncooperative behavior in animals. Am Nat 115:827–857

Clutton-Brock TH (1984) Reproductive effort and terminal investment in iteroparous animals. Am Nat 123:212–229

Clutton-Brock TH (1991) The evolution of parental care. Princeton University Press, Princeton, NJ

Danilowicz BS (1995a) The role of temperature in spawning of the damselfish *Dascyllus albisella*. Bull Mar Sci 57:624–636

Danilowicz BS (1995b) Spatial patterns of spawning in the coral-reef damselfish *Dascyllus albisella*. Mar Biol 122:145–155

Duckworth JW (1992) Effects of mate removal on the behaviour and reproductive success of reed warblers *Acrocephalus scirpaceus*. Ibis 134:164–170

Dunn PO, Hannon S (1992) Effects of food abundance and male parental care on reproductive success and monogamy in tree swallows. Auk 109:488–499

Durand J, Vandel A (1968) Proteus: an evolutionary relict. Sci J 1968:44–49

Godwin J (1995) Phylogenetic and habitat influences on mating system structure in the humbug damselfishes (*Dascyllus*, Pomacentridae). Bull Mar Sci 57:637–652

Gowaty PA (1996) Field studies of parental care in birds: new data focus questions on variation among females. Adv Study Behavior 25:477–531

Grafen A, Sibly R (1978) A model of mate desertion. Anim Behav 26:645–652

Houston AI, Davies NB (1985) The evolution of cooperation and life history in the dunnock, *Prunella modularis*. In: Sibly R, Smith R (eds) Behavioural ecology: the ecological consequences of adaptive behaviour. Blackwell, Oxford, pp 471–487

Kacelink A, Cuthill I (1990). Central place foraging in starlings (*Sturnus vulgaris*). II. Food allocation to chicks. J Anim Ecol 59:655–674

Kawase H, Nakazono A (1995) Predominant maternal egg care and promiscuous mating system in the Japanese filefish, *Rudarius ercodes* (Monacanthidae). Environ Biol Fish 43:241–254

Keenleyside MHA (1991) Cichlid fishes: behaviour, ecology, and evolution. Chapman & Hall, London

Keenleyside MHA, Rangeley RW, Kuppers BU (1985) Female mate choice and male parental defense behaviour in the cichlid fish *Cichlasoma nigrofasciatum*. Can J Zool 63:2489–2493

Kohda M (1988) Diurnal periodicity of spawning activity of permanently territorial damselfishes (Teleostei: Pomacentridae). Environ Biol Fish 21:91–100

Kuwamura T (1996) The evolution of parental care and mating systems among Tanganyika cichlids. In: Kawanabe H, Hori M, Nagoshi M (eds) Fish communities in Lake Tanganyika. Kyoto University Press, Kyoto, pp 57–86

Lavery RJ, Reebs SG (1994) Effects of mate removal on current and subsequent parental care in the convict cichlid (Pisces: Cichlidae). Ethology 97:265–277

Leffelaar D, Robertson RJ (1986) Equality of feeding roles and the maintenance of monogamy in tree swallows. Behav Ecol Sociobiol 18:199–206

Lyon BE, Montgomerie RD, Hamilton LD (1987) Male parental care and monogamy in snow buntings. Behav Ecol Sociobiol 20:377–382

Markman S, Yom-Tov Y, Wright J (1995) Male parental care in the orange-tufted sunbird: behavioural adjustments in provisioning and nest guarding effort. Anim Behav 50:655–669

Markman S, Yom-Tov Y, Wright J (1996) The effect of male removal on female parental care in the orange-tufted sunbird. Anim Behav 52:437–444

Maynard Smith J (1977) Parental investment: a prospective analysis. Anim Behav 25:1–9

Maynard Smith J (1982) Evolution and the theory of games. Cambridge University Press, Cambridge, UK

Meek SB, Robertson, RJ (1994) Effects of male removal on the behavior and reproductive success of female eastern bluebirds *Sialia sialis*. Ibis 136:305–312

Mrowka W (1982) Effects of removal of the mate on the parental care behaviour of the biparental cichlid, *Aequidens paraguayensis*. Anim Behav 30:295–297

Nelson JS (1994) Fishes of the world. Wiley, New York

Randall HA, Allen GR (1977) A revision of the damselfish genus *Dascyllus* (Pomacentridae) with the description of a new species. Rec Aust Mus 31:348–385

Regelmann K, Curio C (1986) Why do great tit (*Parus major*) males defend their brood more than females do? Anim Behav 34:1206–1214

Simon MP (1983) The ecology of parental care in a terrestrial breeding frog from New Guinea. Behav Ecol Sociobiol 14:61–67

Smith JNM, Yom-Tov Y, Moses R (1982) Polygyny, male parental care, and sex ratio in song sparrows: an experimental study. Auk 99:555–564

Stevenson RA (1963) Life history and behavior of *Dascyllus albisella* Gill, a pomacentrid reef fish. PhD thesis, University of Hawaii

Thresher RE (1984) Reproduction in reef fishes. TFH, Neptune City, NJ

Townsend DS (1996) Patterns of parental care in frogs of the genus *Eleutherodactylus*. In: Powell R, Henderson PR (eds) Contributions to West Indian herpetology: a tribute to Albert Schwartz. Society for the Study of Amphibians and Reptiles, Ithaca, New York, pp 229–239

Vehrencamp SL, Bradbury JW (1984) Mating systems and ecology. In: Krebs JR, Davies NB (ed) Behavioural ecology, 2nd edn. Blackwell, Oxford, pp 251–278

Weatherhead PJ (1979) Ecological correlates of monogamy in tundra-breeding savannah sparrows. Auk 96:391–401

Wellington GM, Victor BC (1989) Planktonic larval duration of one hundred species of Pacific and Atlantic damselfishes (Pomacentridae). Mar Biol 101:557–567

Whillans KV, Falls JB (1990) Effects of male removal on parental care of female white-throated sparrows, *Zonotrichia albicollis*. Anim Behav 39:869–878

Winkler DW (1987) A general model for parental care. Am Nat 130:526–543

Wolf L, Ketterson ED, Nolan V Jr (1990) Behavioural response of female dark-eyed juncos to the experimental removal of their mates: implications for the evolution of male parental care. Anim Behav 39:125–134

Wright J, Cuthill I (1989) Manipulation of sex differences in parental care. Behav Ecol Sociobiol 25:171–181

Wright J, Cuthill I (1990) Manipulation of sex differences in parental care: the effect of brood size. Anim Behav 40:462–471