

## An extraordinary life span estimate for the clown anemonefish *Amphiprion percula*

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A population of the clown anemonefish *Amphiprion percula* was studied for 1 year, in Madang Lagoon, Papua New Guinea. From this study, data on mortality events and social structure were used to construct a stage-structured matrix model and estimate the average age at death (life expectancy) of various classes of individuals. Based on this model, it is estimated that the life expectancy of female *A. percula*, the oldest individuals in the population, is 30 years. This estimate is two times greater than the longevity estimated for any other coral reef damselfish and six times greater than the longevity expected for a fish of that size. The result complements the growing body of evidence, from widespread taxa, that organisms subject to low levels of extrinsic mortality show retarded senescence and increased longevity. It is suggested that fishes would be an excellent group for a broad scale comparative test of the predictions of the evolutionary theory of ageing.

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### INTRODUCTION

The evolutionary theory of ageing attributes senescence (age-related physiological deterioration) to the inability of natural selection to eradicate alleles that have deleterious effects later in life (Medawar, 1952; Williams, 1957; Hamilton, 1966; Charlesworth, 1980). The reasoning is that selection will be relatively weak later in life, because extrinsic sources of mortality (*e.g.* predation, starvation, parasites, disease and abiotic factors) will have reduced the proportion of a cohort subject to selection. The theory predicts that in safe habitats, where extrinsic sources of mortality are rare, selection should favour individuals that show delayed senescence (Williams, 1957; Edney & Gill, 1968; Charlesworth, 1980). Further, the theory predicts that the longevity of organisms from safe habitats should be greater than those from less safe habitats. Both predictions

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of the theory have received support ('delayed senescence': Rose, 1984; Austad, 1993; Tatar *et al.*, 1997; Dudycha, 2001 and 'greater longevity': Austad & Fischer, 1991; Rose, 1991; Keller & Genoud, 1997; Sherman & Jarvis, 2002; Blanco & Sherman, 2005), but to determine the robustness of the theory it is important to broaden the taxonomic basis of the support.

The 28 species of anemonefishes (Pomacentridae) found on coral reefs throughout the Indo-Pacific (Allen, 1972; Fautin & Allen, 1992) present an opportunity for a test of the evolutionary theory of ageing in fishes. Anemonefishes are always found in close association with one of 10 species of sea anemone (Fautin & Allen, 1992; Elliott & Mariscal, 2001). Anemones provide the fishes with protection from predators (Allen, 1972; Fautin, 1992); anemonefishes threatened by predators return to the safety of their anemone's tentacles, and fishes removed from the safety of their anemone's tentacles are readily attacked and eaten (Mariscal, 1970; Elliott *et al.*, 1995; Buston, 2003a). The overall rate of mortality amongst these fishes is low when compared to other coral reef fishes (Munro & Williams, 1985; Aldenhoven, 1986; Eckert, 1987; Buston, 2003b). These observations suggest that natural selection will have favoured delayed senescence and increased longevity in the anemonefishes.

In this study, observation of mortality events and information on social structure derived from a 1 year field study of the clown anemonefish *Amphiprion percula* (Lacepède, 1802) are used to construct a stage-structured matrix model and estimate the life expectancy of female *A. percula*. That is, an estimate of the expected average age at death of females, which are the oldest individuals in the population. This estimate is compared to estimates of longevity for other anemonefishes, other coral reef damselfishes and other fishes of similar size. While some caution is required in the interpretation of the results, because they are based on a single year of observations and a small sample, the results are extraordinary and should stimulate further investigation.

## MATERIALS AND METHODS

The key piece of data required to test the evolutionary theory of ageing is the longevity of the species (Austad & Fischer, 1991; Keller & Genoud, 1997; Blanco & Sherman, 2005). Often, estimates of longevity are based on the age of the oldest individual in captivity or the age of the oldest individual found in the field, but these estimates suffer from being based on single individuals. Alternatively, estimates of longevity can be based on estimates of life expectancy of the oldest cohort in a population. The latter estimates of longevity are thought to be good estimates of longevity because they represent the expected average age at death of a number of individuals (Caswell, 2001). The approach has been successfully used to estimate longevity in organisms where ageing by morphological traits is not possible (*e.g.* perennial plants; Ehrlén & Lehtilä, 2002) and in marine organisms living in stable social groups (*e.g.* killer whales; Caswell, 2001). This study uses the latter approach (Cochran & Ellner, 1992; Caswell, 2001), estimating the life expectancy of the oldest cohort of individuals (females) in a population of the clown anemonefish.

## STUDY POPULATION

A population of the clown anemonefish was studied from January 1997 to December 1997, in Madang Lagoon, Papua New Guinea (5°09' S; 145°48' E; Buston, 2002). All

fieldwork was conducted using scuba, at depths of up to 13 m. Ninety-seven groups of *A. percula* were located on three reefs: Sinub (reef 1), Wongad (reef 2) and Masamoz (reef 3) (Jebb & Lowry, 1995). Each group occupied a single anemone *Heteractis magnifica* (Quoy & Gaimard, 1833). Groups consisted of a breeding pair and zero to four non-breeders (mean  $\pm$  s.d. number of individuals in each group =  $3.4 \pm 0.9$ ,  $n = 97$ ).

Individuals  $>18$  mm in standard length ( $L_S$ ) (residents,  $n = 334$ ) could be recognized on the basis of natural variation in their colour markings (Nelson *et al.*, 1994; Elliott & Mariscal, 2001; Buston, 2003a, b). The initial population consisted of 334 residents in 97 groups, but not all individuals could be used to estimate life expectancy because some were removed for experimental tests of other hypotheses (Buston, 2004a, b). These manipulations did not have any effect on the mortality rates of individuals remaining in groups (Buston, 2003b, 2004b). The final sample available to estimate life expectancy was 268 residents in 87 groups.

## MORTALITY EVENTS

Disappearance of residents was monitored by conducting a thorough census of each group every 1 to 2 days, for 302 days (Buston, 2003a, b). If individuals disappeared from their anemone, it was assumed that they had died, rather than migrated. This assumption was based on two empirical results: 1) no individuals that disappeared could be found after a thorough search of all anemones within the study population, indicating that short distance migration did not occur, and 2) no migrants came into the study population from outside, indicating that long-distance migration did not occur (Buston, 2003a). This assumption, that disappearance is equivalent to mortality, gave rise to higher estimates of mortality rate (Buston, 2003b) and will give rise to lower estimates of life expectancy than any other assumption.

## SOCIAL STRUCTURE

Each group of *A. percula* has a well-defined social structure. Within each group, there is a size-based dominance hierarchy (Buston, 2003c; Buston & Cant, 2006); the female is largest (rank 1), the male is second largest (rank 2), and the non-breeders become successively smaller (rank 3 to 6). *Amphiprion percula* is a protandrous hermaphrodite (Fricke & Fricke, 1977; Moyer & Nakazano, 1978); if the female of a group dies, the male changes sex and assumes the position vacated by the female, and the largest non-breeder from the anemone inherits the position vacated by the sex-changing male (Buston, 2004a). The size-based dominance hierarchy reflects a queue for breeding positions (Buston, 2004a). That is to say, new recruits enter a group at the bottom of the hierarchy and only move up through the hierarchy as those ahead die. An individual only becomes female (rank 1) by queuing through the entire hierarchy in its anemone.

## STAGE-STRUCTURED MATRIX MODEL

A transition matrix was constructed based on 1) the observed probability of surviving and maintaining current rank, and 2) the observed probability of surviving and ascending in rank (Table 1). The algorithms described in Cochran & Ellner (1992) and Caswell (2001) for stage-structured matrix models were used to calculate the life expectancy of individuals that attain each rank. The remaining life span of each rank is derived from the transition matrix and its fundamental matrix using a Markov chain, which includes the probabilities that an individual in stage  $j$  at time  $t$  will be in stage  $i$  at time  $t+1$ . The mean age at death of each rank conditional to getting there, that is the life expectancy of each rank was calculated. In the case of rank 1, females, this represents the mean age at death of the oldest class of individuals in the population. To produce a bias-corrected 95% CI for female life expectancy, 2000 bootstrapped matrices

TABLE I. *Amphiprion percula*: the transition matrix shows the probability of surviving, the probability of surviving and maintaining rank, and the probability of surviving and advancing in rank, for each rank based on observations of 268 individuals in 87 groups for 302 days

Transition probabilities	Initial rank					
	6 ( <i>n</i> = 2)	5 ( <i>n</i> = 9)	4 ( <i>n</i> = 25)	3 ( <i>n</i> = 59)	2 ( <i>n</i> = 86)	1 ( <i>n</i> = 87)
Final rank	6	0	0	0	0	0
	5	0	0.4444	0	0	0
	4	0	0.1111	0.7600	0	0
	3	0	0	0.0400	0.8644	0
	2	0	0	0	0.0847	0.8837
	1	0	0	0	0.0581	0.9310
Probability of surviving		0.000	0.5555	0.8000	0.9491	0.9418
					0.9418	0.9310

were generated from original individual data, and the percentile method was used (Efron & Tibshirani, 1993; Caswell, 2001).

## MODEL OUTPUT TRANSFORMATION

The outputs of the model were in the form of cycles of 302 days (the time of the study period), so they were subsequently transformed to provide results in terms of years: 'life expectancy (number of cycles)' times 302 divided by 365. Different group sizes gave rise to different estimates of female life expectancy, so female life expectancy was calculated in groups of two, three, four and five individuals. Since these group sizes ( $G_S$ ) were not equally represented in the population ( $G_S = 1, n = 1$ ;  $G_S = 2, n = 7$ ;  $G_S = 3, n = 48$ ;  $G_S = 4, n = 32$ ;  $G_S = 5, n = 7$ ;  $G_S = 6, n = 2$ ) the results of the model were transformed to produce the life expectancy of the average female: the sum from  $N = 2$  to  $N = 5$  of 'life expectancy (years) in group of size  $N$ '  $\times$  'number of groups of size  $N$ ' divided by the total number of groups. Averaging in this way gave rise to a conservative estimate of female life expectancy.

## RESULTS

### LONGEVITY

For individuals that attain the female position, the remaining life span, or expected time spent as a female is 14.0 years. This expectation does not vary with group size because the mortality rate of females is dependent on rank and rank alone in the model (Buston, 2003b). The life expectancy of females does, however, vary with group size (Fig. 1). This result occurs because, even though the amount of time spent as a female does not vary with group size, the amount of time spent queuing to attain the female position does vary with group size. Accounting for the frequency of groups of different sizes in the population, the average life expectancy of females is 30.8 years (lower 95% CI = 22.0, upper 95% CI = 89.9 years). This life expectancy of the oldest cohort of individuals in the population provides an estimate of longevity.

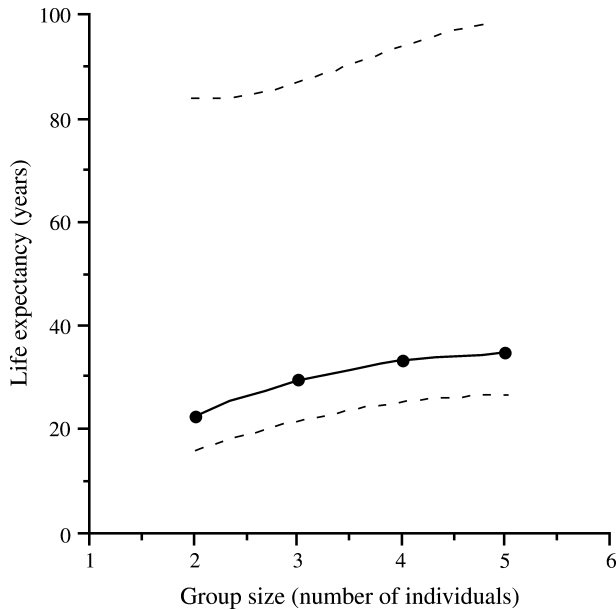


FIG. 1. The life expectancy (—) with 95% CI (---) of female *Amphiprion percula* in groups of two, three, four and five individuals.

## DISCUSSION

The evolutionary theory of ageing predicts that, in species where extrinsic sources of mortality are rare, natural selection should favour individuals that show delayed senescence and increased longevity (Medawar, 1952; Williams, 1957; Hamilton, 1966; Edney & Gill, 1968; Charlesworth, 1980). In light of this, it was predicted that anemonefishes would have an extraordinary longevity, because they live in close association with sea anemones that provide the fishes with protection against predators (Mariscal, 1970; Allen, 1972; Fautin, 1992; Elliott *et al.*, 1995; Buston, 2003*a, b*). In this study, information on mortality events (Buston, 2003*a, b*) and social structure (Buston, 2004*a, b*) of clown anemonefish were used to construct a stage-structured matrix model and estimate the life expectancy of the fish. The life expectancy of females, the oldest individuals in the population, is conservatively estimated to be 30 years. Bearing in mind the weaknesses in the data, which are from 1 year of observations and a small sample, it is reasonable to ask two questions regarding the results: 1) how much confidence can be put in this longevity estimate of 30 years and 2) how can this longevity estimate of 30 years be interpreted?

## VALIDATION

There are three ways to answer the question regarding confidence in the estimate that *A. percula* can live for 30 years. First, the results indicate that the 95% CI of expectancy of female *A. percula* lie between 22 and 90 years. If the question was: how long does *A. percula* live? then the broad range of the

95% CI would be a cause for concern, but because the question is 'Does *A. percula* live a long time?' the broad range matters less. Even being exceptionally conservative it can be concluded that the life expectancy of female *A. percula* is at least 22 years (and is equally likely to be 90 years).

Second, the results are not inconsistent with other observations of anemonefishes, and this lends credence to the idea that the longevity estimate of 30 years is sound. Moyer (1986) reported that an *Amphiprion clarkii* (Bennett, 1830) had lived at least 12 years on a reef in Japan. Fautin & Allen (1992) reported that an *Amphiprion frenatus* Brevoort, 1856, had lived for 18 years and an *Amphiprion perideraion* Bleeker, 1855, had lived for 18+ years, in captivity. These direct observations show that *Amphiprion* sp. are physiologically capable of living a long time. These anecdotal observations might be underestimating longevity because they are based on so few individuals, but they do suggest that the results found here are plausible.

Finally, the results can be considered as a testable prediction. The prediction can be tested by examining validated otolith growth increments (Fowler, 1990; Fowler & Doherty, 1992). There are, however, two potential problems associated with this test. First, growth increments are not always visible in the otoliths of tropical fishes (Panella, 1980; Brothers, 1982; Longhurst & Pauly, 1987). Second, the ethics of sacrificing large number of such a long-lived and highly social species are somewhat questionable. Otoliths were not collected at the time of the study, but it would be interesting to test this hypothesis, in a focused manner, in the future.

## INTERPRETATION

Whether or not the life expectancy estimate for female *A. percula* provides support for the evolutionary theory of ageing depends on how this longevity estimate compares to the longevity estimate of other fishes that are close relatives, other fishes on coral reefs and other fishes that are of a similar size (Sale, 1980; Lowe-McConnell, 1987). The more remarkable estimates of longevity for damselfishes are 10 years for *Pomacentrus wardi* Whitley, 1927 (Fowler & Doherty, 1992), 11 years for *Dascyllus albisella* Gill, 1862 (Hill & Radtke, 1988), 15 years for *Parma victoriae* (Günther, 1863) (Brown, 1982), 15 years for *Stegastes altus* (Okada & Ikeda, 1937) (Kohda, 1996), 17 years for *Hypsypops rubicunda* (Girard, 1854) (Clark, 1970) and 17 years for *Pomacentrus moluccensis* Bleeker, 1853 (Doherty & Fowler, 1994), suggesting that *A. percula* is living two times longer than other damselfishes (Table II).

The longevity of the damselfish *Parma microlepis* Günther, 1862, has been estimated at 37 years (Tzioumis & Kingsford, 1999), but *P. microlepis* is a temperate pomacentrid and temperate fishes are thought to have greater longevity than their tropical counterparts (Lowe-McConnell, 1987). Furthermore, *P. microlepis* is a large pomacentrid (maximum 150 mm  $L_S$ ) and large fishes are thought to exhibit greater longevity than small fishes (Sale, 1980). Indeed, it is estimated that the longevity of fishes of a similar size to *A. percula* (maximum  $L_S$  65 mm) is *c.* 5 years (Blanco & Sherman, 2005), indicating that *A. percula* is living about six times longer than fish of a similar size. All this points to the fact that the life expectancy estimate of 30 years for female *A. percula* is a truly

TABLE II. Longevity estimates of *Amphiprion percula* and other long-lived damselfishes (Pomacentridae), the source of the estimate, their habitat (tropical v. temperate), their size (maximum standard length,  $L_S$ ), and their predicted longevity (+, greater; -, lesser; =, equal) relative to *A. percula* based on habitat and size\*

Damselfish	Source	Habitat	$L_S$ (mm)	Longevity (years)
<i>Amphiprion percula</i>	This study, stage-structured matrix model	Tropical	65	30
<i>Pomacentrus wardii</i>	Fowler & Doherty (1992), otoliths (validated)	Tropical (=)	60 (-)	10
<i>Dascyllus albisella</i>	Hill & Radtke (1988), otoliths (unvalidated)	Tropical (=)	117 (+)	11
<i>Parma victoriae</i>	Brown (1982), scales	Temperate (+)	200 (+) <sup>†</sup>	15
<i>Stegastes altus</i>	Kohda (1996), observation of marked individuals	Temperate (+)	120 (+)	15
<i>Hypsypops rubicunda</i>	Clark (1970), scales	Temperate (+)	300 (+)	17
<i>Pomacentrus moluccensis</i>	Doherty & Fowler (1994), otoliths (validated)	Tropical (=)	90 (+) <sup>†</sup>	17
<i>Parma microlepis</i>	Tzioumis & Kingsford (1999), otoliths (validated)	Temperate (+)	150 (+)	37

\*All else being equal, damselfishes are expected to have similar longevity to *A. percula* due to their shared evolutionary history. Ecological factors are, however, expected to influence longevity: temperate fishes are expected to live longer than tropical fishes; large fishes are expected to live longer than small fishes (Sale, 1980; Lowe-McConnell, 1987).

<sup>†</sup>These estimates of maximum  $L_S$  come from FishBase (<http://www.fishbase.org/search.php>).

remarkable estimate of longevity when compared to other coral reef damselfishes of a similar size (Table II). This supports the idea that the protection from predators afforded by the anemone has resulted in natural selection favouring delayed senescence and increased longevity in the anemonefishes.

The result complements the mounting evidence that organisms subject to lower levels of extrinsic mortality show retarded senescence and increased longevity. Populations of animals, as distinct as opossums, grasshoppers and *Daphnia* sp. that occur in habitats with reduced extrinsic mortality risk, tend to have retarded senescence (Rose, 1984; Austad, 1993, Tatar *et al.*, 1997, Dudycha, 2001). Animals with protective body parts (*e.g.* turtles and porcupines: Rose, 1991), with chemical defences (Blanco & Sherman, 2005), or living in safe habitats (*e.g.* bats: Austad & Fischer, 1991; naked mole-rats: Sherman & Jarvis, 2002), apparently live longer than animals without such protection. Most compellingly, the comparative analysis of Keller & Genoud (1997) indicates that eusociality, and the protection that comes with it, is associated with a 100-fold increase in insect longevity.

A broad scale comparative analysis of longevity among the fishes may provide an excellent test of the ecological predictions of the evolutionary theory of ageing. Such an investigation would be feasible given that many fishes can be accurately aged using their otoliths (Panella, 1980; Brothers, 1982; Longhurst & Pauly, 1987; Fowler, 1990; Fowler & Doherty, 1992). The investigation should minimally control the effect of phylogeny (Felsenstein, 1985; Harvey & Pagel, 1991), body size (Sale, 1980; Blanco & Sherman, 2005), temperate *v.* tropical location (Sale, 1980; Lowe-McConnell, 1987) and the effect of fertility increases with age (Rose, 1991), while testing for an effect of levels of extrinsic mortality.

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