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UNIVERSITY OF PLYMOUTH

PERSONALITY AND PARENTAL CARE IN THE CORKWING WRASSE (*SYMPHODUS MELOPS*)

by

BENJAMIN ALEXANDER ELLIS

A thesis submitted to the University of Plymouth
in partial fulfilment for the degree of

RESEARCH MASTERS

School of Biological and Marine Sciences

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Acknowledgements

Author's Declaration

At no time during the registration for the degree of Research Masters has the author been registered for any other University award without prior agreement of the Doctoral College Quality Sub-Committee.

Work submitted for this research degree at the University of Plymouth has not formed part of any other degree either at the University of Plymouth or at another establishment.

The following external institutions were visited for research and consultation purposes:

Norwegian Institute of Marine Research:

- Austevoll Research Station
- Flødevigen Research Station

Fieldwork, Video Analysis:

Fieldwork: The author participated in the collection of video data in Saltskjærholmane, Austevoll, Norway from May – July 2022.

Video Analysis: The author was solely responsible for the analysis of all baited videos from the 2022 field season, creating full consistency in analysis method and style throughout the video data.

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Personality and Parental care in the Corkwing Wrasse (*Symphodus melops*)

By

Benjamin Alexander Ellis

Abstract

Parental care in many species is a repeatable aspect of the behavioural phenotype, in some cases covarying with other behavioural traits within wider behavioural syndromes. It is well understood that in several freshwater fishes, recreational and commercial fisheries often (directly or indirectly) impact traits concerning parental care adversely, in some cases through selection on covarying behavioural traits. In contrast, studies on commercially fished marine species that exhibit parental care are scarce. The corkwing wrasse (*Symphodus melops*) is a marine fish with complex reproductive behaviour, with parental males exhibiting nest building and parental care behaviours. This species is also subject to a size selective commercial fishery, that makes use of methods known to target bolder and more aggressive individuals. I investigated the boldness and aggression of 14 parental males in the field, while collecting video data of their parental care behaviour. I then tested for relationships between boldness and aggression and three key parental care behaviours, to determine if personality can be linked to parental care quality in this species. My results show consistent repeatable differences between individuals in all tests of boldness and aggression. Additionally, I also suggest that overall bolder individuals exhibit higher quality of parental care while more aggressive individuals exhibit a reduction in quality. This study provides the first

evidence of personality influencing parental care behaviours in this species, as well as highlighting

the potential impacts of this link in the context of fisheries-induced selection.

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1. Introduction

Parental care is an invaluable part of the life history of many organisms, both terrestrial and aquatic. It allows the care-giving individual or individuals to increase their fitness by enhancing the survival of offspring, using a variety of behaviours that provision the young with resources essential to their development and protect them from threats (Gross 2005; Mann 2009; Jamieson 2009; Royle et al. 2012). Parental care strategies are many and varied across taxa with the burden of parental care falling to females (maternal) in some cases, males (paternal) in others, or may be shared between both parents (biparental); in some cases parental care is even provided to non-descendant offspring (alloparental care). However, for teleost fishes that exhibit parental care, the male is the sole carer in approximately 61% of species (Blumer 1982; Ahnesjö 1992; 2008). Parental males exhibit a broad range of strategies to care for and protect their young (Turner 1986, 1993; Sargent and Gross 1993), from the specialised brood pouches of male sygnathids (Carcupino et al. 2002; Stölting and Wilson 2007), to the mouthbrooding catfish (*Genidens genidens*) which forgo feeding to protect their young (Barbieri et al. 1992). One particularly interesting and complex life-history strategy is that shown by nesting fishes. These species construct elaborate nests for both courtship and parental care, and often show diverse reproductive phenotypes. However almost all research on such systems have been focused on freshwater species. Centrarchids, such as the bluegill sunfish (*Lepomis macrochirus*), pumpkinseed sunfish (*Lepomis gibbosus*), largemouth bass (*Micropterus salmoides*), and smallmouth bass (*Micropterus dolomieu*) are the most well-studied species in this context. These species are found in diverse freshwater habitats from ponds and lakes to streams and rivers (Lee 1980; Berra 2001). Despite this diversity in habitat, these species demonstrate several key similarities. They all exhibit sexual size and male dimorphisms, with larger dominant parental males, smaller females, and smaller subordinate sneaker males. Parental and sneaker males exhibit

different reproductive strategies, parental males construct nests by digging depressions in sediment, removing silt and sand as well as plant and algal species, leaving a bed of coarse rock and gravel that require constant maintenance to ensure it remains exposed (Morgan 1951; Turner and MacCrimmon 1970; Heidinger 1975; Avila 1976; Baylis et al. 1993). Once completed females will then approach the nest and be courted by the male, with successful courtship resulting in the near simultaneous release of gametes into the nest, where the eggs will adhere to the exposed rocky substrate. Parental males guard the eggs until the larvae fully disperse, protecting the brood from predators and provisioning them via aeration through fanning behaviour (Pflieger 1966; Philipp et al. 1997). However, during the release of gametes, sneaker males will attempt to steal fertilisations from the parental male, releasing sperm into the nest to fertilise the newly released eggs, allowing them to avoid the costly parental care process (Gross 1979; Gross and Charnov 1980; Baylis et al. 1993; Neff and Knapp 2009).

The aforementioned species are also all frequently subject to size-selective recreational, and at times commercial, fisheries with the largest individuals being disproportionately targeted by anglers (Goedde and Coble 1981; Coble 1988). As a result, such populations can be subject to a phenomenon known as fisheries-induced evolution (FIE) (Heino & Godø, 2002). Under the framework of FIE, selection acts upon a suite of physiological and behavioural traits, selecting for individuals with slower growth rates, earlier sexual maturation and reduced adult body size, which can reduce the reproductive potential of a population (Heino and Godø 2002; Kuparinen and Merilä 2007; Sutter et al. 2012; Twardek et al. 2017a). In species that exhibit sexual dimorphism, size selective fisheries are also likely sex selective (Rowe and Hutchings 2003; Fenberg and Roy 2008; Kendall and Quinn 2013), therefore larger parental males are subject to greater selection intensity compared with females and sneaker males. Fisheries-induced evolution is also now understood to be able to act, directly or indirectly, on consistent individual differences in

behavioural traits, termed personality traits or behavioural syndromes when there is significant covariation among personality traits (Sih et al 2004; Toms et al. 2010; Sih 2013; Twardek et al. 2017a). Réale *et al.* (2007) outlined five key personality trait axes of interest to behavioural ecologists: boldness, aggressiveness, sociability, exploration, and activity. Of these axes, boldness and aggression are relevant as they are recognised to have evolutionary and ecological significance in the context of parental care and FIE. Boldness is the propensity of an individual to take risks (Wilson and Godin 2009), while aggressiveness is how agonistic an individual is in its response to a conspecific (Réale et al. 2007). In centrarchids and other fishes, recreational angling has been shown to disproportionately target individuals based on behaviour type (often the most aggressive and boldest males) (Wilson et al. 2015; Twardek et al. 2017a, Monk et al. 2021), which can impact the quality of parental care. In many cases, the targeted bolder and more aggressive males are also better able to defend their nest from predators and provision their young through fanning (Uusi-Heikkilä et al. 2008; Wilson and Godin 2009; Wilson et al. 2011; Philipp et al. 2015).

Despite the breadth of this research on freshwater species, research on similar marine species is largely lacking. For example, the corkwing wrasse (*Symphodus melops*), is found in coastal waters around the North Sea and north-east Atlantic (Knutsen et al. 2013; Mattingsdal et al. 2019) and is known to also exhibit sexual and male dimorphism with larger, brightly coloured parental males, smaller, more dull females, and sneaker males, that mimic the external morphology of females (Potts, 1974; Sayer et al. 1996; Uglem et al. 2000). Interestingly, corkwing wrasse exhibit similar, but more complex nest building behaviour compared to centrarchids. For example, between May and July, parental males will construct 1-3 large, elaborate nests comprised of diverse (i.e. > 10 species) specifically selected algae that weigh up to 1.5 kilograms (Potts 1974, 1985). Parental males will specifically select certain types of algae for their physical properties, often collecting and transporting large amounts of such algal material around the habitat.

In terms of reproduction, corkwing wrasse are very similar to centrarchids. Females will approach the nest of a parental male, engage in courtship, eventually resulting in the release of gametes into the nest. Sneaker males will also often attempt to steal fertilisation by divebombing the nest at the moment fertilisation occurs and releasing sperm (Potts 1974, 1985; Uglem et al. 2000). Following fertilization, parental males will then encapsulate the eggs within a protective layer of algae within the interior of his nest using existing or new algal material from within his territory (Potts 1974, 1985). The male will then maintain the structure of the nest, provision the developing larvae via aeration through fanning behaviour, and protect them from predation for approximately 2 weeks, before repeating the process (by either reusing his current nest or constructing a new nest nearby) (Potts 1974, 1985). Unlike the freshwater species however, which experience high levels of egg predation from other species, corkwing wrasse larvae experience predation predominantly from conspecifics.

This species is also subject to an intense size-selective commercial fishery in both Scandinavia and the United Kingdom for use as a biological control for ectoparasitic copepods in salmon aquaculture (Halvorsen et al 2016, 2017a, b). This fishery has implemented a minimum size limit of 12cm as a conservation measure (Halvorsen et al 2016, 2017a, b), however this disproportionately targets larger parental males, resulting in fisheries-induced selection, potentially leading to FIE and the suite of negative impacts associated with it (Halvorsen et al 2016, 2017a, b). This fishery makes use of baited pots known as wrasse traps; such passive fishing methods are known to select for bolder and more aggressive individuals (Biro and Post 2008; Uusi-Heikkilä et al. 2008). Due to this, corkwing wrasse populations are potentially being subject to a selection pressure against bold and aggressive individuals, potentially reducing parental care quality as seen in freshwater species. Yet despite their ecological and commercial importance, the link between these behavioural traits and parental care behaviours has never been studied.

In this study, my primary aim was to ascertain whether parental male corkwing wrasse exhibit consistent individual differences in boldness and aggression, and further, understand how these personality traits influence three key parental care behaviours: fanning quality, rate of foraging-based maintenance (FBM), and rate of non-foraging-based maintenance (NFBM). To achieve this, firstly video data of these behaviours was collected from the field over a 30-day period from 14 individuals. Secondly, to assess individual boldness, two tests were used: latency to return to the nest after a predatory stimulus, and latency to return after the placement of a model of a parental male. Finally, to assess individual aggression, a further two tests were used: latency to first direct attack on parental male model, and frequency of direct attacks on parental male model over a 3-minute period. I predicted that both bolder and more aggressive individuals would provide a higher quality of fanning (Uusi-Heikkilä et al. 2008; Wilson and Godin 2009; Wilson et al. 2011; Philipp et al. 2015) and would be more likely to forage for new nesting material when repairs were necessary rather than using material from within the nest site, therefore showing an increased rate of FBM, but a decrease in rate of NFBM. Understanding the link between personality and parental care in this species is imperative to produce more detailed fisheries assessments and conservation legislature, to ensure that this fisheries impact on corkwing wrasse populations is sustainable.

2. Materials and Methods

2.1. Data Collection

2.1.1. Collection Site

Data were collected from the southwestern shore of the island of Saltskjærholmane (60°4'54.11''N, 5°17'24.219"E) in Austevoll western Norway between 31st May 2022 and 8th July 2022 (Figure 1). The collection site is protected from commercial fishing and during the breeding season (1st May to 30th July) is home to a high-density population of nesting corkwing wrasse.

Figure 1: (A) Map of Norway with the location of Saltskjærholmane. (B) The island of Saltskjærholmane, with the sample site marked. Scale bar = 100m.

2.1.2. Nest Selection

Corkwing wrasse nests form prominent domed structures with a diameter of approximately 40cm throughout the study site and can be identified visually from the surface. Potential nests were therefore identified through two snorkelling surveys of the study area. Nests were selected for video recording if a dominant male was present within the nest, the nest had a clear entrance and was in

an area where camera rigs could be placed. Nests were given a unique ID prior to recording and their GPS coordinates were recorded, with a total of 19 nests being recorded across the study period.

2.1.3. Nest Filming

Nests were filmed using ten waterproof cameras (GoPro HERO7 and HERO9) attached to weighted camera rigs, constructed using a weighted flat plastic platform with camera mounted on top (Figure 2). A buoy was connected to the rig using approximately eight meters of rope for retrieval and identification. Each rig contained a single camera which recorded 70-100 minutes of 4K 30 FPS video per deployment. Cameras were deployed 40 – 60cm from the nest via snorkelling with the camera facing the entrance to the nest. Cameras were collected approximately two hours later to allow for the maximum recording time. Nests were filmed between 31st of May 2022 and 8th July 2022. Nests were selected for filming if a dominant male was present within the nest, if the dominant male was not seen in a nest for two consecutive filming sessions then it was deemed abandoned and the closest nearby nest was selected to be filmed from that point on. The deployment time of cameras varied significantly due to changes in environmental conditions throughout the field season, deployment occurred from 9:14 – 16:41, with the average deployment time being 12:34. A maximum of 10 Nests were filmed daily, with fewer being recorded towards the end of the breeding season as less males were engaged in nesting behaviour.
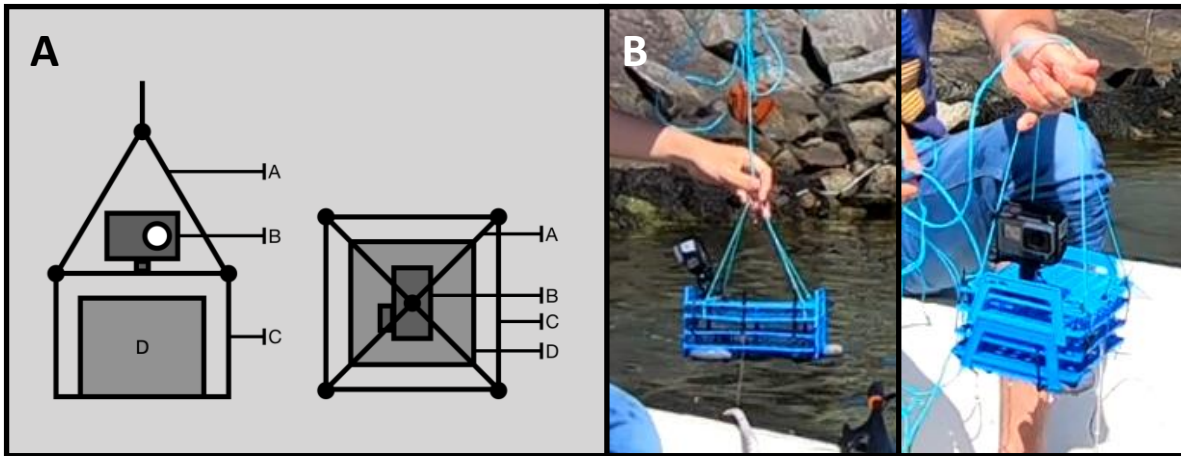
Figure 2: (A) Diagram of the camera rig used for nest footage collection. (A) Rope, (B) GoPro/Camera, (C) Plastic Platform, (D) Weight. (B) Camera rig as deployed in the field.

2.1.4. Behavioural Trait Tests

To quantify the boldness of parental males I tested the latency to return to the nest after a simulated predator attack, and after introducing a conspecific to the nest. The first test utilised a 3m pole that was rapidly moved into the nest entrance, to mimic the attack of a large predator such as a diving bird (Figure 3C). Secondly a 25cm model showing a photograph of a parental male in mating colouration was placed in the nest entrance, to mimic a competitor engaged in egg predation (Figure 3B, D). The model was placed in the nest entrance for 6 minutes to allow adequate time for male to volitionally return to the nest and interact with the stimulus.

To quantify the aggression of parental males I recorded two measures of agonistic behaviour towards the model conspecific. First, I recorded the latency between the male first returning to the nest after model placement, and the first bite attack on the model (Figure 3D). Secondly I recorded the frequency of bite attacks for 4 minutes after the parental male first returns to the nest.

The pole test was performed daily, immediately after camera placement. Whereas the model tests were conducted every 2 days to minimise habituation and were performed after a full round of pole tests had been conducted.
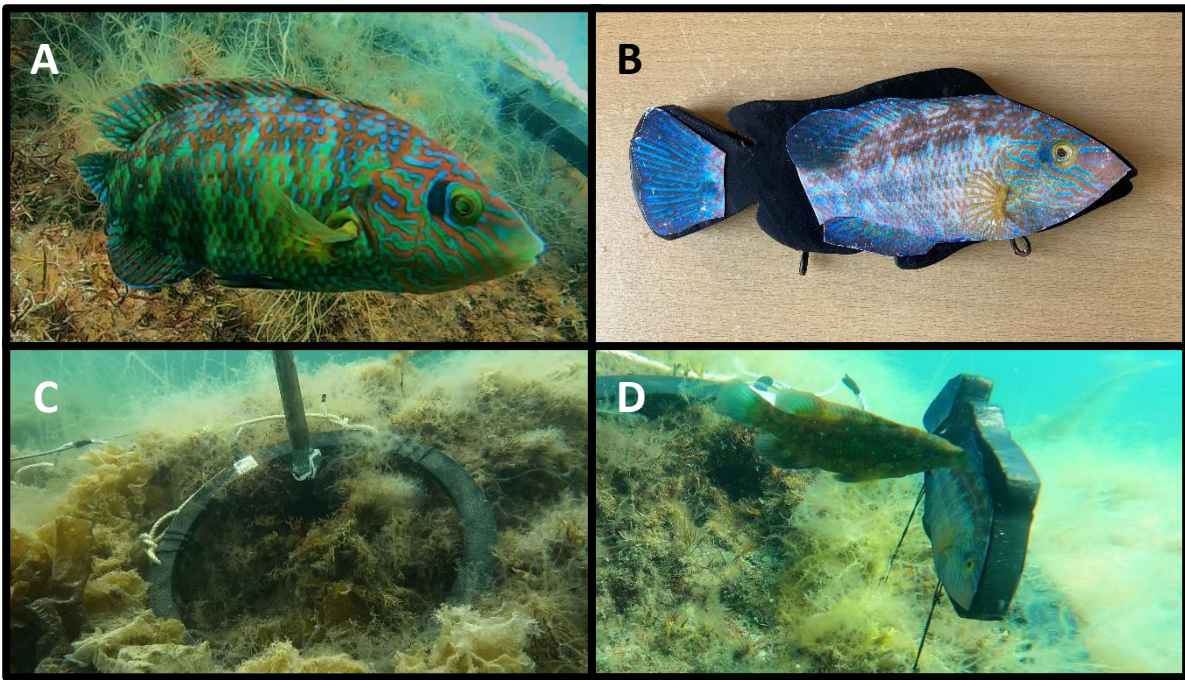
Figure 3: (A) Parental male corkwing wrasse (*Symphodus melops*) in spawning season colouration. (B)

Model parental male corkwing wrasse used as a conspecific in behavioural trait tests (25cm in length). (C)

Pole test being conducted, with pole (top centre frame) being lowered rapidly into the nest entrance

(centre frame). (D) Model conspecific deployed in the field with parental male engaged in a bite attack.

2.2 Analyses

2.2.1. Video Analysis

Behavioural analysis was performed using the program BORIS – Behavioural Observation Interactive Software (Friard and Gamba 2016). A total of 127 videos were analysed from 16 nests, sorted by nest ID. 3 Nests were excluded from analyses as the nest entrance was obscured making parental care behaviours impossible to record. Each nest was recorded an average of 10 times for 90 minutes, with an average of 11 hours of footage per nest.

2.2.2. Parental Male Identification

Parental males make use of multiple nests per season, therefore individual parental males were identified based on their unique facial patterns, in order to group together observations of the same male from a different nest. In total 2 males were captured at multiple nests, resulting in data on 14 individuals being collected.

2.2.3. Selection of Parental Care Traits

Parental care quality was measured using three metrics: (1) Fanning quality: defined as the average rate of pectoral fin rotations per second of dominant male time present at the nest. (2) Rate of foraging-based maintenance (FBM): The average rate at which the male brought foraged material back to the nest site and incorporated said material into the nest structure per hour. (3) rate of non-foraging-based maintenance (NFBM): The average rate at which the male incorporated material from within the nest site back into the nest structure per hour.

2.2.4. Data Analysis

Data was processed in BORIS and then extracted as an observation list. Behavioural interactions were organised by nest ID for investigation, two types of behaviours were recorded, point behaviours (behaviours that have no duration) and state behaviours (behaviours that take place

over a period). For point event behaviours, frequency was recorded, for state behaviours, total duration was recorded and percentage of male time at the nest under the criteria of the behaviour was calculated.

2.2.5. Statistical Analysis

Data analysis was carried out in R software (R version 4.0.4; The R Foundation for Statistical Computing 2021). The package rptR was used to first quantify the repeatability of the four behavioural traits under test, by extracting the intra-class correlation coefficient (ICC) of each, and its 95% confidence intervals (Table 1). Then the package glmmTMB was used to calculate multiple generalised linear mixed models to determine the relationship between each repeatable behavioural trait (treated as fixed effects) and parental care metrics (treated as response variables). The day of the experiment was also included as a fixed effect in the models to account for changes in the environmental conditions at the study site over the period of the experiment, while random intercepts were included to account for the clustering of data on male ID. Initial analysis indicated that for certain metrics of parental care males differed in how their parental care changed over the course of the experiment. Therefore, in addition to random intercepts on male ID, I also included random slopes across day of the experiment for each male, where appropriate. Delta AIC was used to determine the best random effects structure and which fixed effects should be retained from saturated models. To aid model interpretation, significance values for retained fixed effects were obtained using likelihood ratio tests.

3. Results

3.1. Repeatability of Behavioural Trait Tests

Responses of individuals to all 4 behavioural trait tests were shown to be significantly repeatable, based on non-overlap of zero by the lower 95% confidence interval (Table 1). Individual differences accounted for 49.7% of the variation in observed in pole test return time, 49.7% of the variation in model test return time, 49.3% of the variation in latency to first attack and 48.4% of the variation in frequency of attacks in 4 minutes.

Table 1: Repeatability of behavioural trait tests, ICC values and 95% confidence intervals presented.

Test	Trait Tested	ICC	95% CI
Pole Return Test	Boldness	0.50	0.21 – 0.67
Model Return Test	Boldness	0.50	0.16 – 0.68
First Attack Latency Test	Aggression	0.49	0.15 – 0.70
Frequency of Attacks Test	Aggression	0.48	0.15 – 0.69

3.2. Relationships with Fanning Quality

Fanning quality showed a positive relationship with model test return time (χ^2_1 = 4.04, p < 0.05; Figure 4B) and a near-significant negative trend with pole test return time (χ^2_1 = 3.28, p = 0.07; Figure 4A). Fanning quality did not vary across days (Model Test: χ^2_1 = 0.06, p = 0.80; Pole Test: χ^2_1 = 1.69, p = 0.19), but there was an interaction between day and model test return time (χ^2_1 = 4.58, p < 0.05; Supplementary Figure 1). For the first measure of aggression, attack latency, there was no relationship with fanning quality (χ^2_1 = 0.87, p = 0.35; Figure 4C) and although day had a significant effect on fanning quality in this model (χ^2_1 = 4.04, p < 0.05) there was no interaction between day and attack latency (χ^2_1 = 2.99, p = 0.08). Finally, fanning quality declined with increasing attack frequency (χ^2_1 = 5.10, p < 0.05; Figure 4D), but there was no effect of day (χ^2_1 = 2.66, p = 0.10).
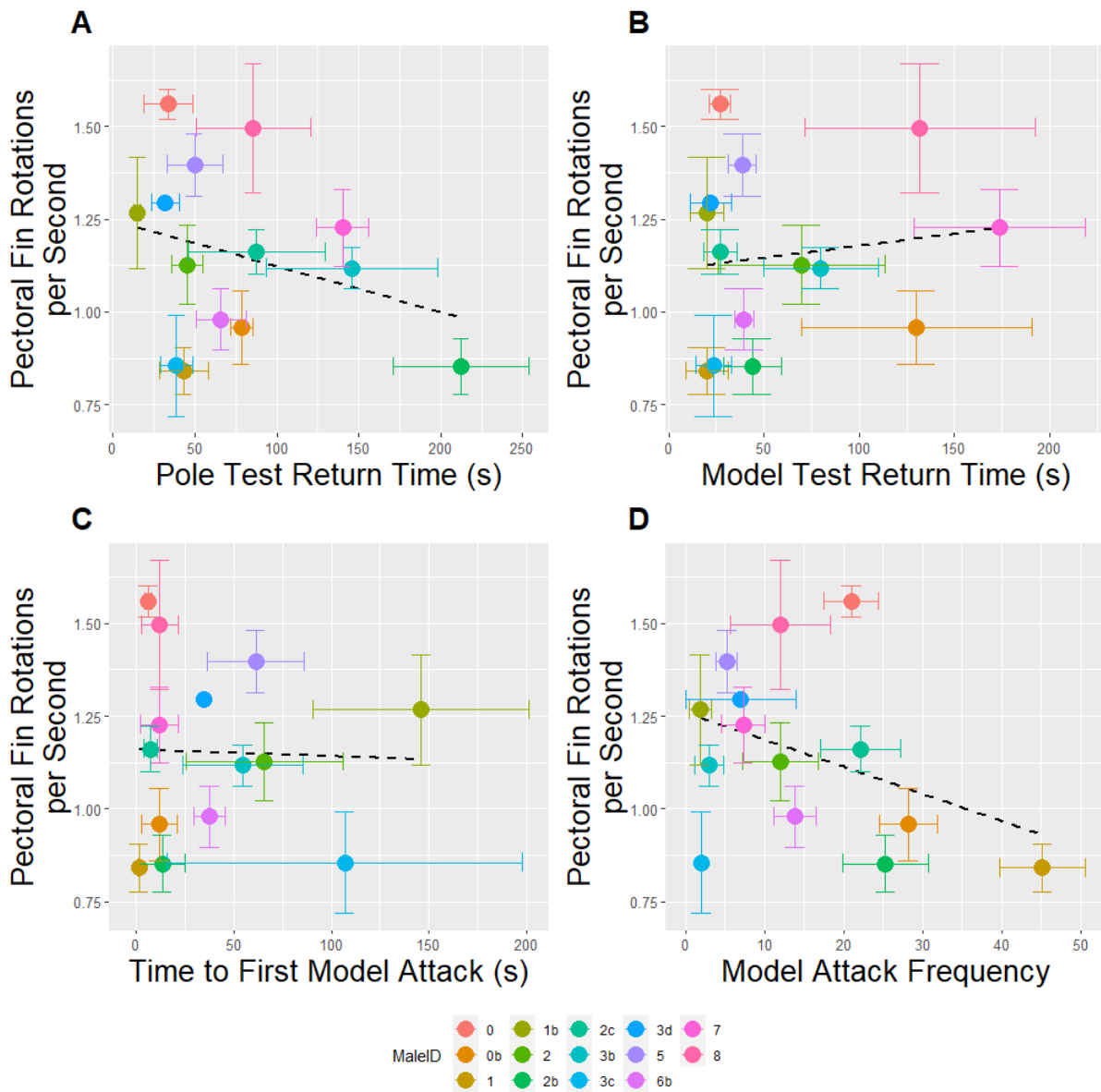
Figure 4: Relationship between: Fanning quality and (A) Pole test return time. (B) Model test return time.

(C) Time to first model attack. (D) Frequency of attacks in 240 seconds. Lines of best fit were calculated

using least squares regression (n=14). Each data point represents the mean value of each behaviour for a

different male in the sample. Error bars show SE.

3.3. Relationships with Foraging-Based Maintenance

Rate of FBM showed no relationship with pole test return time ($\chi^2_1 = 0.27$, $p = 0.60$; Figure 5A) but did show a significant negative relationship with day ($\chi^2_1 = 4.81$, $p < 0.05$), and there was a near-significant interaction between day and pole test return time ($\chi^2_1 = 3.52$, $p = 0.06$). Model test return time did not vary with rate of FBM ($\chi^2_1 = 0.30$, $p = 0.59$; Figure 5B), day ($\chi^2_1 = 0.11$, $p = 0.74$), and there was no interaction between day and model test return time ($\chi^2_1 = 0.96$, $p = 0.33$). There was also no relationship between attack latency and rate of FBM ($\chi^2_1 = 0.05$, $p = 0.46$; Figure 5C) or day ($\chi^2_1 = 0.77$, $p = 0.38$). Finally, there was no relationship between frequency of attack and rate of FBM ($\chi^2_1 = 0.69$, $p = 0.41$; Figure 5D), and as above there was no effect of day on rate of FBM ($\chi^2_1 = 1.12$,

Figure 5: Relationship between: Rate of foraging-based maintenance (FBM) and (A) Pole test return time. (B) Model test return time. (C) Time to first model attack. (D) Frequency of attacks in 240 seconds. Lines of best fit were calculated using least squares regression (n=14). Each data point represents the mean value of each behaviour for a different male in the sample. Error bars show SE.

3.4. Relationships with Non-Foraging-Based Maintenance

Rate of NFBM showed a negative relationship with pole test return time (χ^2_1 = 7.75, p < 0.01; Figure 6A), and with day (χ^2_1 = 6.82, p < 0.01), there was also a highly significant interaction effect between pole return time and day (χ^2_1 = 19.54, p < 0.01; Supplementary Figure 2). Model test return time did not show a relationship with rate of NFBM (χ^2_1 = 2.62, p = 0.11; Figure 6B), with day also not showing a relationship with rate of NFBM (χ^2_1 = 0, p = 1.00), however, there was an interaction effect between model test return time and day (χ^2_1 = 6.83, p < 0.01; Supplementary Figure 3). For the aggression tests, attack latency showed no relationship with rate of NFBM (χ^2_1 = 1.36, p = 0.24; Figure 6C), and day had no effect on rate of NFBM in this model (χ^2_1 = 0.68, p = 0.41). Attack frequency also showed no relationship with rate of NFBM (χ^2_1 = 0.02, p = 0.88; Figure 6D), with day having a near-significant negative relationship with rate of NFBM (χ^2_1 = 3.59, p = 0.06).

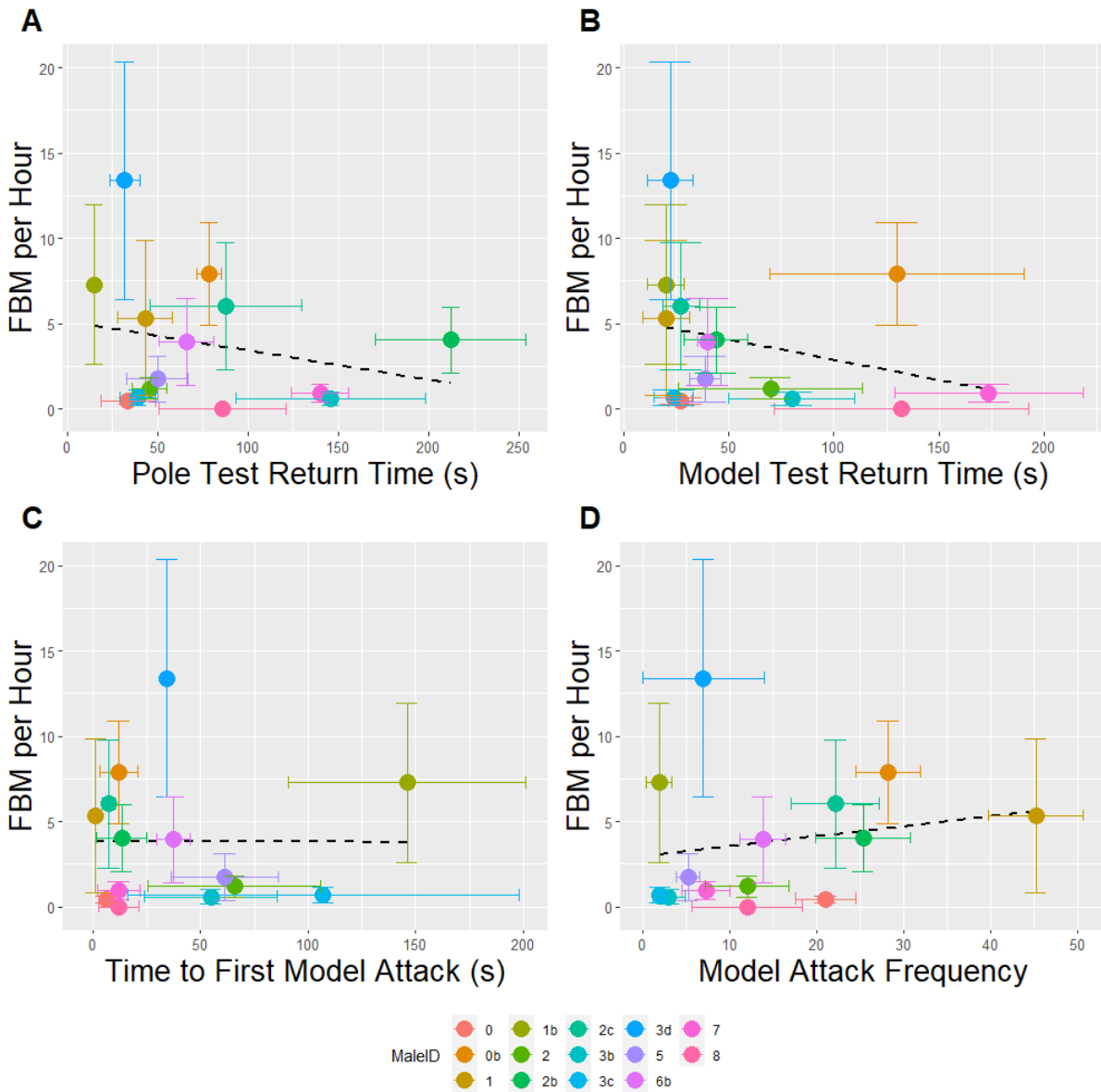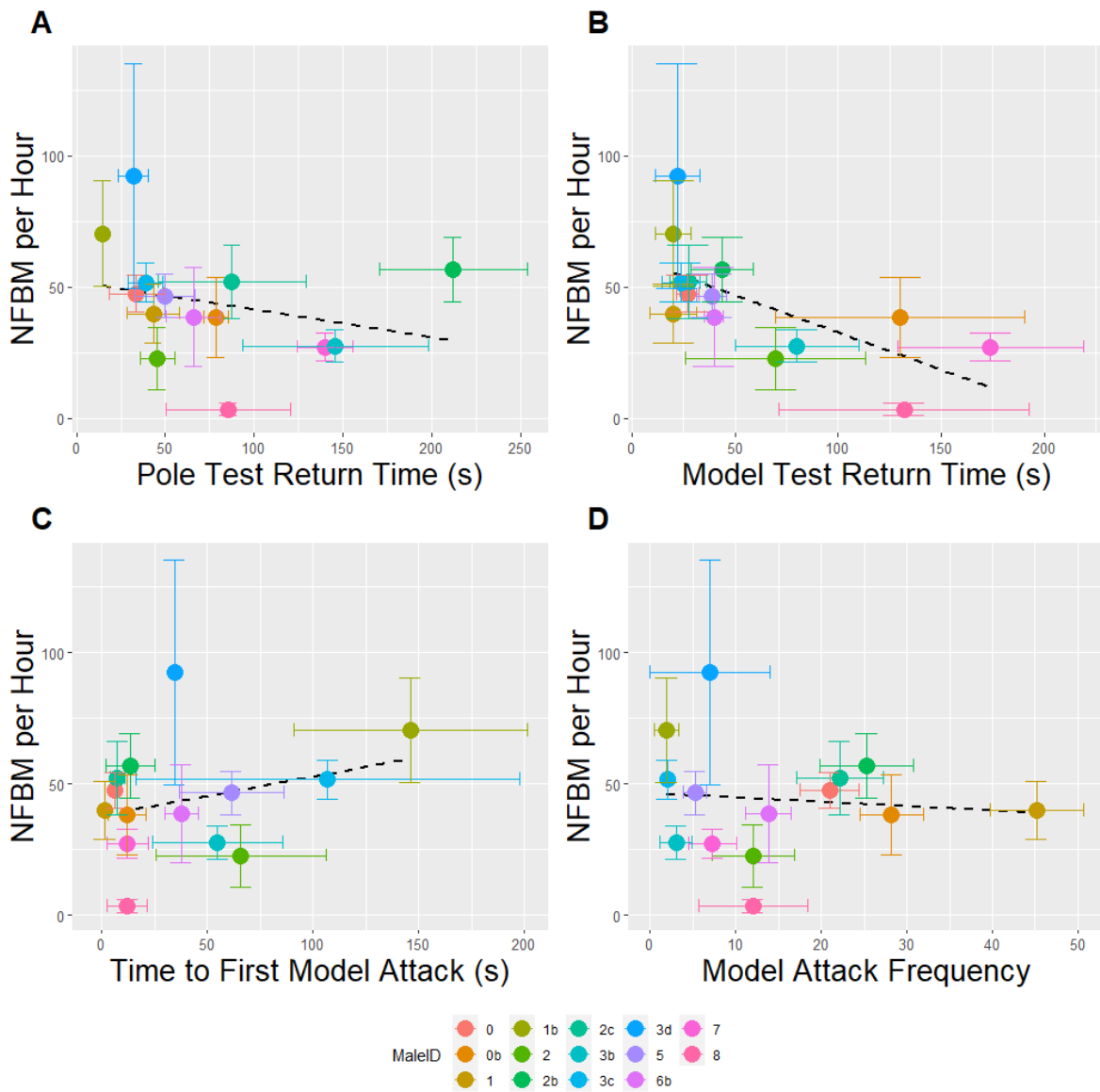**Figure 6:** Relationships between: Rate of non-foraging-based maintenance (NFBM) and (A) Pole test return time. (B) Model test return time. (C) Time to first model attack. (D) Frequency of attacks in 240 seconds. Lines of best fit were calculated using least squares regression (n = 14). Each data point represents the mean value of each behaviour for a different male in the sample. Error bars show SE.

4. Discussion

The results of this study show that parental male corkwing wrasse demonstrate consistent individual differences in measures of boldness and aggression. Furthermore, boldness was correlated with two measures of parental care quality (fanning quality and rate of NFBM), while aggression was correlated with one (fanning quality), indicating that these personality traits are embedded in a wider behavioural syndrome. Bolder individuals demonstrated reduced fanning quality, but also showed an increase in rate of non-foraging-based maintenance, while more aggressive individuals also showed a reduction in fanning quality. The key parental care behaviours investigated are essential for reproductive success in this species. Commercial fishery practices that target this species are known to use methods that can disproportionately select for bolder and more aggressive individuals, driving indirect fisheries-induced selection for less bold and less aggressive individuals, which my results suggest may potentially influence the parental care traits of this species in several ways.

Contrary to my initial prediction, parental males that exhibited a lower latency to return to the nest after the placement of a model conspecific also showed reduced fanning quality; suggesting that bolder parental males exhibit reduced fanning quality. However, this relationship varied significantly between days (Supplementary Figure 1), from days 5 to 11 a positive trend was seen, but from days 13 to 27 an opposite negative trend was seen. The presence of this temporal variation suggests that I should proceed with caution when interpreting my overall relationship, as it is possible that my observation window did not fall on a period that best represents the overall direction of this relationship. Corkwing wrasse exhibit periodic spawning cycles where behavioural frequency in known to vary (Karaszkiewicz 2020; Supplementary Figure 4), the observed variability may be due to this effect, but could also be due to environmental factors such as warming temperatures towards the latter half of the sampling period. However, despite being non-significant, latency-to-

return after the pole test suggested a near-significant opposite trend suggesting that bolder dominant males exhibit higher quality fanning behaviour, while also showing no significant variation in this relationship between days. Bolder parental male centrarchids show increased levels of agonistic behaviour, better defending their nests from primarily allospecific brood predators (Sutter et al. 2012; Philipp et al. 2015; Twardek et al 2017a, b), however in corkwing wrasse, brood predators are primarily conspecifics (Uglem et al. 2000; Halvorsen 2017a). The pole and model tests investigate different aspects of boldness, the pole tests for a parental males' latency to return after a momentary attack on the nest by a large predator (e.g., a diving bird or heron), whereas the model tests for his latency to return while a conspecific is present within his nest. To return to the nest in both scenarios poses a risk, however only in the model test is the risk still present and visible to the parental male after initial stimulus presentation. Corkwing wrasse nesting sites are often densely populated with multiple parental males moving around the site foraging for new material. A bolder male would therefore be expected to risk agonistic engagements with extant threats to his nest more frequently, therefore reducing the time budget available for fanning behaviour, which may explain the observed relationship.

The relationship between attack frequency on the model conspecific also supports this explanation as the most aggressive parental males (those that performed the most attacks) also showed lower overall fanning quality (Figure 4D). This suggests that more aggressive parental males are more willing to engage in prolonged contests, so they also likely have reduced time budget for engaging in fanning behaviour. Overall, these results suggest that bolder and more aggressive parental males exhibit reduced fanning quality due to males making a trade-off, reducing offspring provisioning in favour of increased nest defence. Parental males with the lowest latency-to-return after the pole test showed an increased rate of NFBM (Figure 6A), while latency to return after the model was placed exhibited a very similar trend but was non-significant (Figure 6B), however this relationship

varied across days in both tests. The temporal variation between pole test return time and rate of NFBM showed no apparent pattern but generally indicated that bolder males provide an increased rate of NFBM (Supplementary Figure 2). While the relationship between model test return time and NFBM, showed a consistent relationship across all days, bar two where only one male was sampled (Supplementary Figure 3), therefore I suggest that the observed significant variation is likely a statistical artifact generated by these two data points. Consequently, providing further evidence that my overall relationship is indeed representative of this relationship. The similarity between these two trends provides evidence that bolder parental males might maintain their nest at a higher quality than less bold males, repairing damage and maintaining structure more frequently. The nest of the corkwing wrasse is complex, using specific species of live algae to fulfil certain purposes. For example, *Mastocarpus stellata* is primarily used to cushion and protect developing eggs in the interior of the nest, while encrusting *Corallina officinalis* forms the structural and defensive outer layers, with this material continuing to grow even after it is placed in the nest (Potts 1985). Nest structure is constantly threatened from damage via predation, environmental damage, and overgrowth of algal material. Therefore, constant nest maintenance is essential to protect and ensure the correct development of the eggs within. Parental males are also often observed removing algal material from the nest and discarding it (Bussmann et al. 2021), this is likely the removal of dead algal material, as decomposition may result in a reduction in dissolved oxygen available for developing larvae, potentially leading to hypoxia, which has a suite of negative impacts for larval development (Rombough 1988a, b; Keckeis et al. 1996; Hassel et al. 2008a; 2008b; Wood et al. 2019). Centrarchids are also known to suffer from brood parasites (Kat 1984), due to the similarities between these species corkwing wrasse may face similar threats, with increased maintenance potentially reducing the risk of larval mortality posed by parasites. These results therefore suggest that bolder males better maintain their nests, providing their eggs with greater

protection from predation and environmental threats, while likely reducing the risk of impaired larval development and mortality.

Overall, I did not find a relationship between boldness and FBM as I had predicted. Studies of centrarchids have shown that bolder individuals perform maintenance more frequently (Philipp et al. 2015; Twardek et al. 2017a, b), however this behaviour differs in two distinct ways between centrarchids and the corkwing wrasse. Firstly, maintenance in centrarchids consists of intense fanning of the caudal fins to remove sediment (Pflieger 1966), whereas here I look at the gathering of algal material from outside the nest and its subsequent addition to its structure. Secondly, centrarchids nest on substrates consisting of sand and gravel, corkwing wrasse however, predominantly use rocky substrates which are occasionally connected to sandy substrates. These differences in the complexity and the context of this behaviour may account for the lack of a relationship. Despite this I do see similar trends to those seen in centrarchids in my data, which suggested that bolder males do perform maintenance with foraged material more frequently (Figure 5A, B). Foraging-based maintenance is comparatively rare compared to NFBM (occurring approximately one tenth as frequently), consequently the differences between individuals are less defined. This behaviour is also exhibited most frequently at the start of a nesting cycle, during nest construction and early spawning events, therefore capture of behaviour during this period is preferred, however this period varies by male during the spawning season and cannot be predicted with any certainty. Clarifying the nature of this relationship is essential as FBM has not only impacts for larval development and survival but also for the role corkwing wrasse play as ecosystem engineers. Parental males move large quantities of algal material around their habitat during FBM and any change in frequency of this behaviour could have unknown consequences at an ecosystem level. Future work might be able to clarify the nature of this relationship, and through collection of

data on additional individuals, to reveal if factors such as sample size and collection date might have influenced my result.

While there was also no observed relationship between either FBM or NFBM and my tests of aggression, they do exhibit similar trends which suggest aggressive males generally perform less maintenance (Figure 5C, D, Figure 6C, D). This trend is likely also due to more aggressive parental males trading off other nest care behaviours for increased nest defence, reducing the time available for maintenance. It could also be suggested that the nests of more aggressive parental males receive less damage from predation and sneaker male attacks due to their increased aggression, reducing the amount of maintenance necessary to keep the nest in good condition. The inclusion of data on additional parental males by future work may also be able to reveal the true nature of this relationship, and what factors influenced my current results.

The corkwing wrasse is subject to a size selective commercial fishery that has been shown to reduce wrasse density in heavily fished areas (Halvorsen et al. 2016, 2017a, b). This fishery primarily uses methods shown to disproportionately target bolder and more aggressive individuals in other species (Wilson et al. 1993; Carter et al. 2012; Michelangeli et al. 2016), it is therefore likely that fished wrasse populations experience fisheries-induced selection against bold and aggressive personalities, although the nature of this relationship in corkwing wrasse should be investigated through future study. Here I have shown that parental male corkwing wrasse have distinct behavioural types that can influence their parental care behaviour. These results suggest that the selective removal of bold and aggressive individuals would alter parental care behaviours exhibited by parental males, reducing the rate of nest maintenance, while increasing the quality of fanning, but likely at the expense of anti-predator behaviours. Together these impacts may lead to an increase in larval mortality, reduced growth rates and increased larval deformities all of which act to reduce the fitness of the parental male, consequently leading to increased rates of nest

abandonment and loss of the developing brood (Taborsky et al. 1987; Stiver et al. 2018; Alonzo 2004). These factors may act to accelerate population declines in fished populations through reducing their reproductive success, and genetic diversity, resulting in the reduced commercial viability of this fishery while negatively impacting the ecological function of corkwing wrasse as a key ecosystem engineer.

This study presents evidence on previously unstudied interactions between key behavioural traits and reproductive behaviours in a fished marine species. For the first time quantifying the relationships between two axes of personality and parental care in the commercially fished corkwing wrasse, showing the potential for a fisheries impact. Consequently, understanding how the levels of boldness and aggression vary between fished and non-fished populations is essential for the introduction of effective fishing quotas and protective legislature, to minimise this impact of this aspect of fisheries-induced selection. Propensity for exploration may be critical in understanding how populations can adapt to increased fishing pressures and the changes in climate through migration, which is already being seen in corkwing wrasse populations (Knutsen et al. 2013). While this study outlines how differences in behavioural type can impact several parental care behaviours, several trends in the data remain inconclusive, further studies to augment this dataset using past and future observations on additional individuals, may help to elucidate the true nature of these relationships allowing for more accurate conclusions to be drawn.

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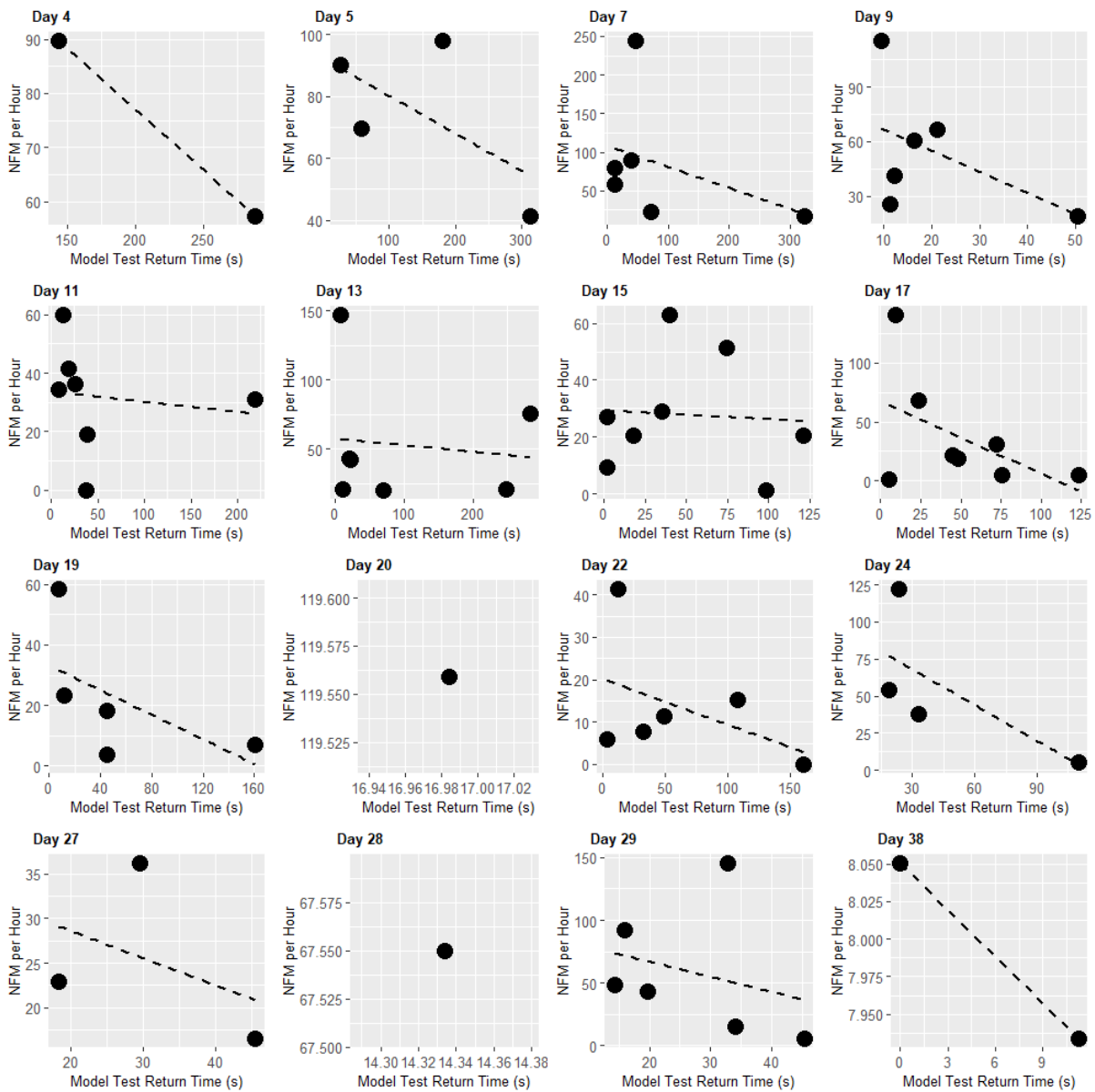
6. Appendices
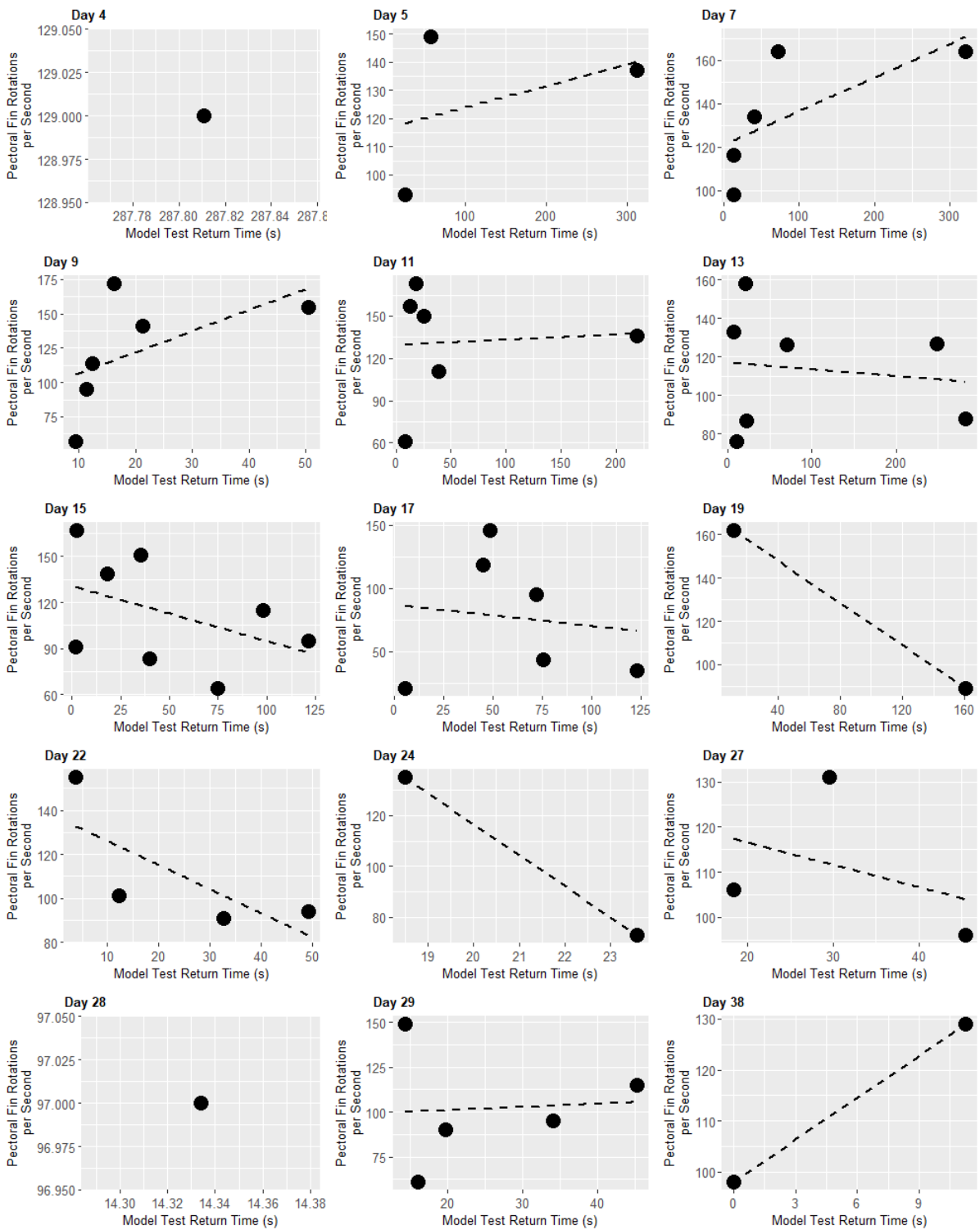
Supplementary Figure 1: Relationships between model test return time and fanning quality on each day the model test was performed. Each point represents and individual parental male.
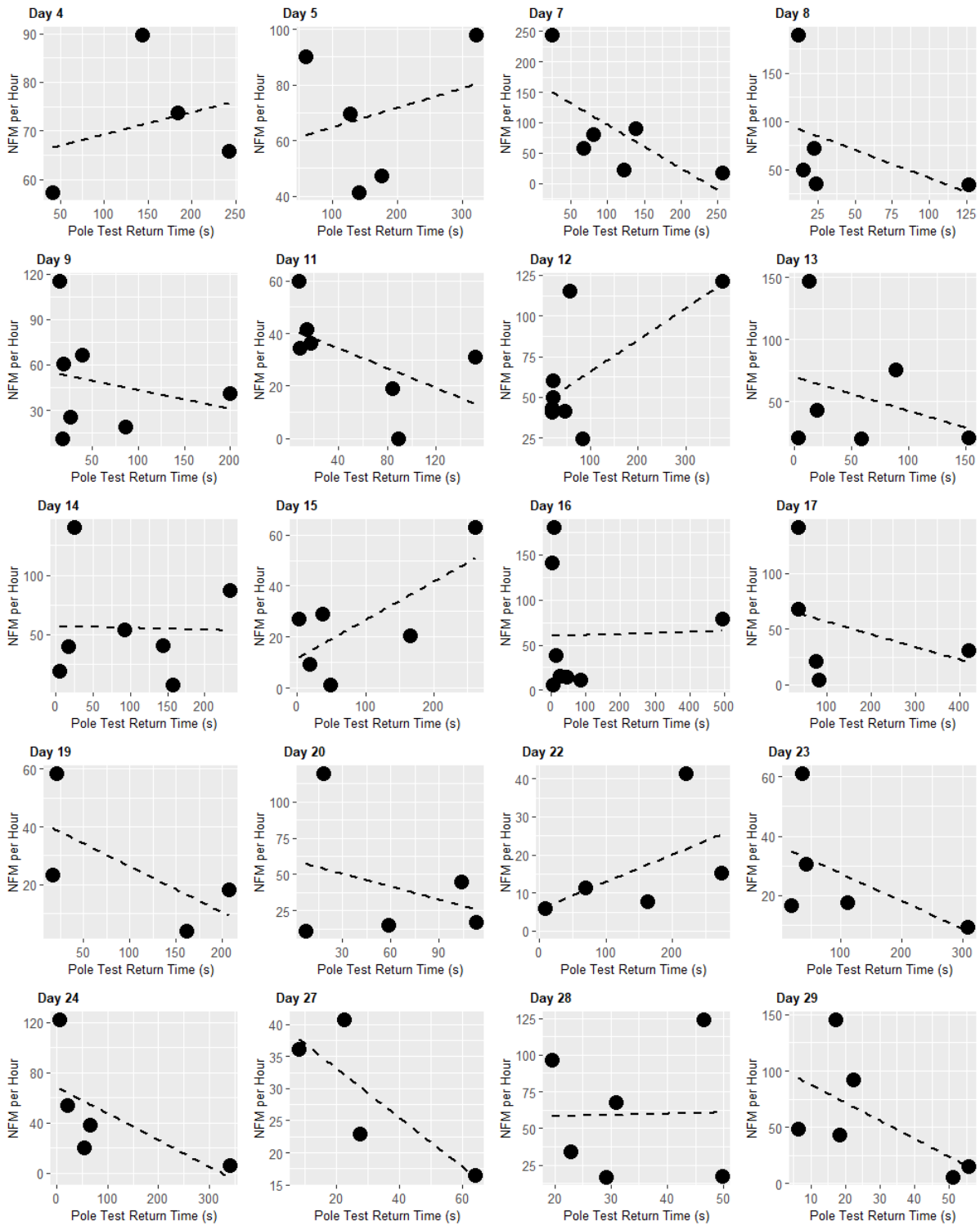
Supplementary Figure 2: Relationships between pole test return time and non-foraging-based maintenance on each day the pole test was performed. Each point represents and individual parental male.

Supplementary Figure 3: Relationships between model test return time and rate of non-foraging-based maintenance on each day the model test was performed. Each point represents and individual parental male.
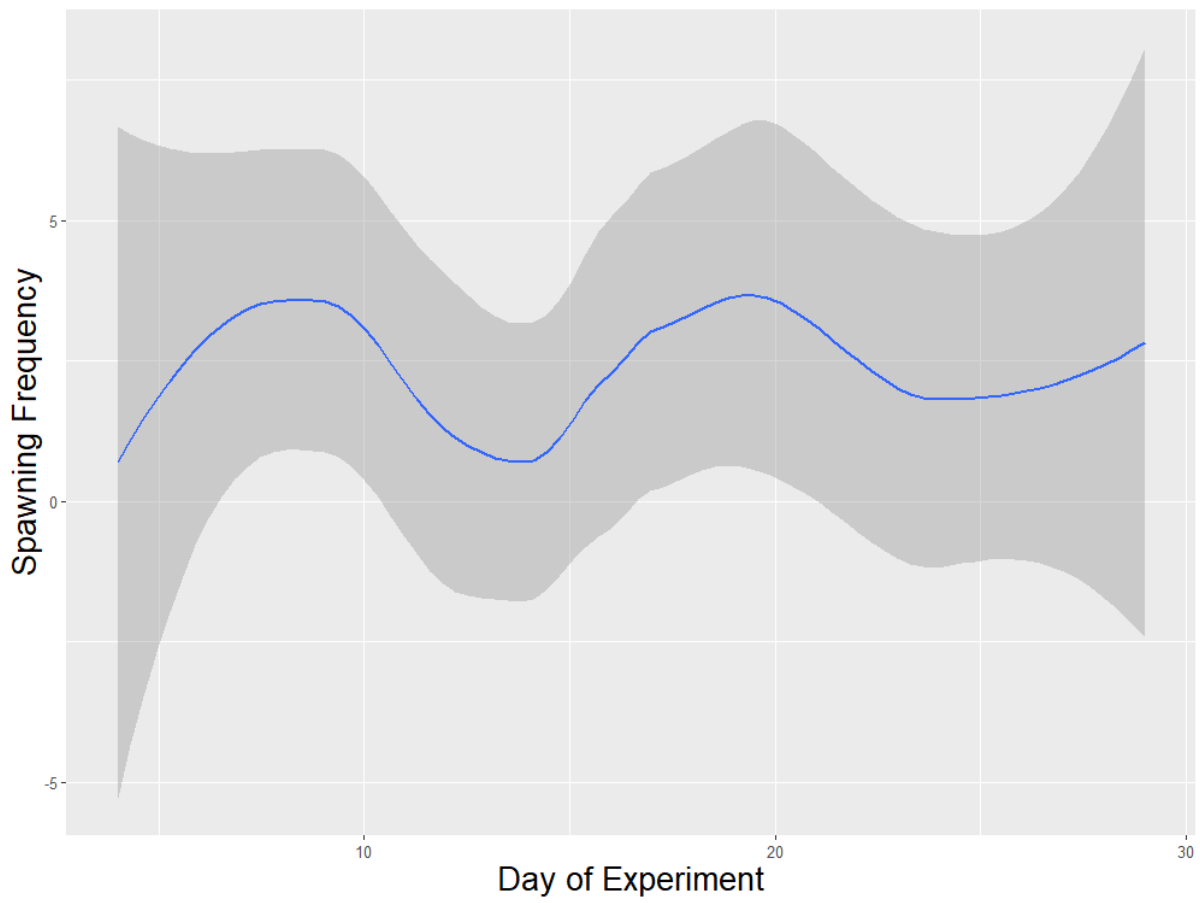
Supplementary Figure 4: Variation in parental male spawning frequency over time.