

Year-round sexual harassment as a behavioral mediator of vertebrate population dynamics

VICTORIA J. WEARMOUTH,^{1,7} EMILY J. SOUTHALL,¹ DAVID MORRITT,² RICHARD C. THOMPSON,³ INNES C. CUTHILL,⁴
JULIAN C. PARTRIDGE,⁴ AND DAVID W. SIMS^{1,5,6}

¹Marine Biological Association of the United Kingdom, The Laboratory, Citadel Hill, Plymouth PL1 2PB United Kingdom

²School of Biological Sciences, Royal Holloway, University of London, Egham TW20 0EX United Kingdom

³Marine Biology and Ecology Research Centre, School of Marine Science and Engineering, Marine Institute, University of Plymouth, Drake Circus, Plymouth PL4 8AA United Kingdom

⁴School of Biological Sciences, University of Bristol, Woodland Road, Bristol BS8 1UG United Kingdom

⁵Ocean and Earth Science, National Oceanography Centre, University of Southampton, Waterfront Campus, European Way, Southampton SO14 3ZH United Kingdom

⁶Centre for Biological Sciences, Institute for Life Sciences, Building 85, University of Southampton, Highfield Campus, Southampton SO17 1BJ United Kingdom

Abstract. Within-species sexual segregation is a widespread phenomenon among vertebrates, but its causes remain a topic of much debate. Female avoidance of male coercive mating attempts has the potential to influence the social structure of animal populations, yet it has been largely overlooked as a driver of sexual separation. Indeed, its potential role in long-term structuring of natural populations has not been studied. Here we use a comparative approach to examine the suitability of multiple hypotheses forwarded to account for sexual segregation (i.e., activity budget, predation risk, thermal niche–fecundity, and social factors) as drivers underlying sex-specific habitat use in a monomorphic model vertebrate, the small-spotted catshark, *Scyliorhinus canicula*. Using this hypothesis-driven approach, we show that year-round sexual habitat segregation in *S. canicula* can be accounted for directly by female avoidance of male sexual harassment. Long-term electronic tracking reveals that sperm-storing female catsharks form daytime refuging aggregations in shallow-water caves (~3.2 m water depth) and undertake nocturnal foraging excursions into deeper water (~25 m) on most nights. In contrast, males occupy deeper, cooler habitat (~18 m) by day and exploit a range of depths nocturnally (1–23 m). Males frequent the locations of shallow-water female refuges, apparently intercepting females for mating when they emerge from, and return to, refuges on foraging excursions. Females partly compensate for higher metabolic costs incurred when refuging in warmer habitat by remaining inactive; however, egg production rates decline in the warmest months, but refuging behavior is not abandoned. Thermal choice experiments confirm that individual females are willing to “pay” in energy terms to avoid aggressive males and unsolicited male mating attempts. Long-term evasion of sexual harassment influences both the social structure and fecundity of the study population, with females trading off potential injury and unsolicited matings with longer-term fitness. This identifies sexual harassment as a persistent cost to females that can mediate vertebrate population dynamics.

Key words: behavior; dimorphism; elasmobranch; habitat and social segregation; mammal; sex; sexual conflict; shark; small-spotted catshark; *Scyliorhinus canicula*; telemetry.

INTRODUCTION

Sexual segregation is the separation of a species such that the sexes live apart, either singly or in single-sex groups. In some species, sexual segregation emerges as a tendency for individuals to segregate into single-sex groups or, in solitary species, to avoid members of the opposite sex (termed social segregation), whereas in other situations, the sexes differ in their use of the physical environment (habitat segregation). However, these categories are not mutually exclusive, as socially

segregating species may also exhibit sex-specific habitat use (social and habitat segregation). Within-species sexual segregation is a widespread phenomenon among vertebrates (Ruckstuhl and Neuhaus 2005), but its causes remain a topic of debate (Ruckstuhl and Clutton-Brock 2005). Because this behavior has implications for the biology, ecology, and management of many species (Pérez-Barbería et al. 2007), it would be beneficial to understand the driving mechanisms. As a result, this topic has received a great deal of interest in recent years, with much attention being devoted to understanding sexual segregation in group-living ungulate (hoofed) mammals. Several explanatory hypotheses have emerged from this research, with those that have received the most support focusing on sex differences in

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⁷ E-mail: vjwearmouth@gmail.com

TABLE 1. Summary of assumptions and key predictions of the five hypotheses forwarded to account for sexual segregation (adapted from Wearmouth and Sims [2008]).

Hypothesis	Assumptions	Predictions
Predation risk hypothesis	Females and/or their offspring are more at risk to predation than males. Male reproductive success is influenced by condition.	Females select "safer" habitats to maximize reproductive output. Males exploit areas where resources are abundant.
Forage selection hypothesis	There are sex differences in nutritional requirements as a result of body size dimorphism or reproductive demands (e.g., gestation).	Sex differences in prey selection result from sex- or reproductive-mode-specific habitat use or competitive exclusion from preferred resources.
Activity budget hypothesis	Sex differences in body size or reproductive investment result in sex-specific activity budgets, making synchronization of behavior costly and, for solitary species, leading to divergent habitat requirements.	High fission rates in mixed-sex groups lead to the formation of unisexual groups. Solitary species exhibit size- or reproductive-mode-specific habitat use.
Thermal niche–fecundity hypothesis	Ambient temperature influences fecundity and sex differences exist in the temperature at which fecundity is maximized.	The sexes select different thermal habitats in an effort to maximize reproductive success.
Social factors hypothesis	Social affinity (intrasexual cooperation or information transfer) or aversion (avoidance of aggression) determine social groupings.	Groups comprise individuals of varying ages (experience) and in many cases are related. The "aggressor" is aggressive and dominant to the "avoider."

predation risk, forage selection, and activity budgets (Conradt 2005, Wearmouth and Sims 2008). Here we provide a brief overview of each of the hypotheses forwarded to account for sexual segregation; for a detailed review of all hypotheses, see Wearmouth and Sims (2008). The key assumptions and predictions of each hypothesis are summarized in Table 1.

The *predation risk hypothesis* focuses on sex differences in the way animals strive to maximize their lifetime reproductive success. It is assumed that females and/or their offspring are more at risk than males of being preyed upon; thus, while male habitat use is driven by resource availability, female habitat choice is driven by a necessity to reduce the risk of predation and thereby maximize offspring security. Investigations into the underlying causes of sexual segregation in ungulates provide the most convincing support for the predation risk hypothesis. For example, male mule deer, *Odocoileus hemionus*, have been documented to obtain a higher quality diet than females, which stay close to water (to satisfy the high water demands of lactation) and occupy habitats with increased shrub cover and a reduced density of both conspecific males and predatory coyotes, *Canis latrans* (Main and Coblenz 1996). The predation risk hypothesis is also applicable to situations in which males experience higher predation as a result of female-biased body size dimorphism. For example, male guppies (*Poecilia reticulata*) are both smaller and more colorful than females and, as a result, occupy shallower, marginal habitats than females to evade fish predators when the risk of predation is high (Croft et al. 2004).

Under the *forage selection hypothesis* it is assumed that sex-related differences in body size or reproductive strategy (for example, female provisioning for offspring) confer significant differences in nutritional needs and/or foraging efficiency. It is therefore predicted that the sexes select alternative habitats to meet their differing

resource requirements, leading to habitat segregation of the sexes. For example, the degree of sexual segregation exhibited by red deer (*Cervus elaphus*) on the Isle of Rhum, UK, has been shown to increase during winter, with increasing population density, and to be most pronounced for animals feeding on short grasslands. It was therefore concluded that stags were less tolerant of low plant biomass and were excluded from mutually preferred communities by indirect competition (Clutton-Brock et al. 1987). Among other animal groups, sexual body size dimorphism appears to favor the larger-bodied sex in terms of foraging advantages. For example, due to mass-related changes in heating and cooling rates, only large male Galapagos marine iguanas, *Amblyrhynchus cristatus*, are able to forage subtidally, where food availability and consequential intake rates are increased (Wikelski and Trillmich 1994).

Sex differences in body size also underlie the *activity budget hypothesis*, as consequential sex-specific activity budgets (including movement rates) make synchronization of behavior costly. As a result, it is predicted that high fission rates arise where the sexes co-occur, leading to social segregation and the formation of unisexual groups. Support for the activity budget hypothesis comes from the observation of significant differences in the activity budgets of male and female bighorn sheep, *Ovis canadensis*, with females spending more time foraging and walking and having longer bouts of both than do males (Ruckstuhl 1998). Similarly, the activity of red deer in mixed-sex groups is significantly less synchronized than that of deer occurring in single-sex groups (Conradt 1998). However, the activity budget hypothesis has received some criticism; it has been suggested that activity budgets are inherently flexible and are not fundamental attributes of animals (Mooring and Rominger 2004), and thus are unlikely to drive segregation of the sexes.

The *thermal niche-fecundity hypothesis* arose from investigations into the presence of sexual segregation in ectotherms. Like the predation risk hypothesis, this hypothesis focuses on intraspecific differences in the way the sexes strive to maximize their lifetime reproductive success. However, it is assumed that sex differences occur in the temperature at which fecundity is maximized and thus that the sexes occupy different thermal habitats in an attempt to maximize reproductive output (Sims 2005). This hypothesis remains largely unexplored due to its relatively recent formulation, but it could explain sex differences in residency times of Atlantic cod (*Gadus morhua*) on spawning grounds: while males remain resident, it is believed that females may move into warmer waters to “incubate” developing eggs before subsequently returning to aggregation sites for spawning (Robichaud and Rose 2003). The application of the thermal niche-fecundity hypothesis does not appear to be confined to ectotherms; temperature may also play an important role in habitat selection of some mammals. For example, pregnant and lactating female little brown bats, *Myotis lucifugus*, have high energy demands through the summer and must remain homeothermic, whereas males often exhibit diurnal torpor, leading to sexual segregation by altitude (Altringham and Senior 2005).

Although a lack of support for the thermal niche-fecundity hypothesis may be partially attributable to its recent formulation, the same cannot be said of the long-standing *social factors hypothesis*. This hypothesis assumes that individuals form single-sex groups due to social affinities or avoidance behavior (Conradt 2005). The formation of same-sex groups may enable reproductively naïve individuals to locate suitable breeding sites and potential breeding partners, or may reflect the need for males to develop fighting skills, establish dominance relationships, and evaluate potential rivals. Alternatively, sexual segregation may reflect the avoidance of intersexual aggression, such as the aggressiveness of females during parturition, or female avoidance of sparring males. However, this hypothesis has been largely overlooked as a putative driver of sexual separation. Indeed, its potential role in the long-term structuring of natural populations has not been studied (Wearmouth and Sims 2008). This may be attributable to the fact that many species investigated thus far typically exhibit sexual body size dimorphism. Sex differences in body size are likely to confer significant sex differences in attributes such as predation risk, nutritional requirements, and activity budgets, all of which can influence spatial and temporal habitat use by the sexes (Tufto et al. 1996, Ruckstuhl 1998, Martin et al. 2003). Therefore, sexually size-dimorphic species may not be the most appropriate models for examining differences due to sex per se. Social aversion has been suggested to underlie sexual segregation in the sexually size-dimorphic guppy (*Poecilia reticulata*) during short-term experiments in a seminatural system (Darden and

Croft 2008). Nonetheless, it remains unclear whether intersexual avoidance could drive sexual segregation in wild animal populations over the long term.

For the majority of animal species, the sexes exhibit differential investment in reproduction (Parker 2006), which leads to sexual conflict (Chapman et al. 2003) and can promote sexual coercion. Sexual harassment, in which males consistently court and attempt to mate with females, is likely to incur significant costs to both sexes (Magurran and Seghers 1994). Although males are able to trade off the costs (e.g., lost feeding opportunities) and benefits (increased fecundity) of coercing females to mate, females must either endure or avoid unwanted attention from males and its associated costs, e.g., increased predation risk, energetic expenditure, disease transmission, reduced fecundity, foraging efficiency, and even injury and death (Daly 1978, Clutton-Brock and Parker 1995, Stockley 1997). Female avoidance of male coercive mating attempts has the potential to influence the social structure of animal populations (Clutton-Brock and Parker 1995) and, as such, intersexual avoidance may be an important mechanism underlying population structuring for many species. This is particularly likely for species such as sharks that show aggression during courtship and copulation (Sims 2005). Fertilization in sharks is internal (Dodd 1983) and involves complex courtship and mating behaviors (Carrier et al. 1994), including male biting of the female to manipulate her position prior to mating. Consequently, mating incorporates considerable physical exertion and is often highly aggressive, with females bearing significant injuries.

In this study we examine the causes of sexual habitat segregation in a model vertebrate predator species, the small-spotted catshark, *Scyliorhinus canicula*, which is sexually monomorphic with respect to body size. Previous field observations in a tidal marine lake demonstrated movements of *S. canicula* over a limited (two-week) period that were consistent with habitat segregation of the sexes; adult males occupied home ranges in open seabed habitat and adult females aggregated within small caves, termed refuges (Sims et al. 2001). It has been suggested previously that, because female *S. canicula* store active sperm (Metten 1939a, b) and copulation need not precede every ovulation in this species, females may refuge to limit injurious and energy-demanding mating activity (Sims et al. 2001). However, because the mating period is protracted in this species (male *S. canicula* carry sperm reserves all year; Garnier et al. 1999), habitat separation would be expected to persist year-round if it were driven by mating avoidance. Here we investigate, for the first time, the temporal stability of sexual habitat segregation in *S. canicula* and, using a multiple-hypothesis-testing approach, we examine four of the five hypotheses forwarded to account for sexual segregation to explore why females segregate from males and refuge in caves. The forage selection hypothesis is not examined, as several previous studies (e.g., Ellis et al. 1996, Sims et

al. 2001), including a study parallel to the current one (D. Morritt, *unpublished data*), have shown no sex differences in prey selection in this species. We examine whether the sexes occupy different habitats due to sex differences in activity budgets that would make coordination of behavior between the sexes difficult (activity budget hypothesis); whether females refuge to avoid predators (predation risk hypothesis); whether female catsharks select warm-water refuges to maximize rates of reproductive output (thermal niche–fecundity hypothesis); or, alternatively, whether the formation of female-only aggregations functions to reduce levels of male harassment to individual females (social aversion hypothesis) and thus is a principal factor underlying this pattern.

MATERIALS AND METHODS

Study species

The small-spotted catshark (*Scyliorhinus canicula* L.) (Chondrichthyes: Elasmobranchii) is a small-bodied (<1 m total length) benthic shark found over sand, gravel, and mud bottoms at 3–110 m depth in the Western Atlantic (Norway to West Africa) and Mediterranean (Wheeler 1969, Compagno 1984). Like the majority of scyliorhinids, it is an oviparous species, laying pairs of egg cases, one per oviduct at a time, which the female anchors to macroalgae and sessile invertebrates in shallow water (Ellis and Shackley 1997). *S. canicula* is an opportunistic feeder (Lyle 1983) with a diet composed principally of mollusks and crustaceans, but that also includes polychaete worms and a variety of small demersal bony fishes (Wheeler 1969, Compagno 1984). As it is the most abundant catshark species in European inshore waters (Ellis and Shackley 1997) and it is a small-bodied, generalist predator that survives well in captivity, *S. canicula* provides a useful model species for laboratory behavioral experiments.

Shark capture

The movements and behavior of wild male and female catsharks were monitored in Lough Hyne, southwest Ireland (Fig. 1). Two-week field visits were undertaken in each seasonal quarter (winter, January; spring, April/May; summer, July; autumn, October) over a two-year period (April 2003–January 2005). Catsharks were captured using gill nets (stretched mesh size 80 mm), deployed for short soak times (mean 110 min), principally in slope habitats (net mean depth between 4 and 9 m) during the hours of darkness. Laboratory experiments were conducted at the Marine Biological Association (MBA) Laboratory in Plymouth, UK, where fish were obtained by short (40-min) otter trawls during research surveys in local coastal waters.

Acoustic and archival telemetry of free-ranging catsharks

During April 2003, 10 adult catsharks (5 male, 5 female) were fitted with temperature and depth-logging data storage tags (LTD_2400, Lotek Wireless, Newmarket, Ontario, Canada) and between April 2003 and

January 2004, 18 adult catsharks (8 male, 10 female) were fitted with coded acoustic pingers (V16, Vemco, Halifax, Nova Scotia, Canada). All tags were placed intraperitoneally (for detailed methodologies, see Sims et al. 2006). Archival tags recorded swimming depth every 10 min for up to 1 year, whereas acoustic tags monitored horizontal movements for up to 2 years by recording presence within the vicinity (~200 m detection radius; Wearmouth 2006) of acoustic receiver stations (VR2, Vemco, Canada) moored in nonoverlapping locations in open seabed habitats and outside a female refuge (G1) (see Fig. 1).

Archival data analysis

Change in depth between successive 10-min intervals was used as a proxy for activity (Sims et al. 2006). To examine long-term (monthly to annual) patterns in activity, a double-plot actogram was constructed for each fish by summing binary activity (1 = active, 0 = inactive) over sequential 2-h periods. A one-way ANOVA with Minitab 14.13 (Minitab 2004) was used to investigate sex differences in square-root transformed mean daily activity (change in depth) over a 10-d period during summer.

Data storage tag data were also used in an empirical model of catshark metabolism to estimate the energy expenditure of actual swimming movements occurring in the thermal habitats occupied by each fish. Energy expenditure attributable to standard metabolism (R_s , metabolic rate at zero swimming speed) was determined for each fish at each 10-min interval for the duration of tag deployment using the oxygen consumption–body mass relationship at 15°C derived for *S. canicula* as given in Sims (1996):

$$\dot{V}O_2 = 0.104M^{0.855}$$

where $\dot{V}O_2$ is oxygen consumption in mg O_2 /h and M is mass in grams. Fish in the current study were of similar mass (~800 g), allowing direct comparison between individual catsharks. However, this linear (log–log) relationship between body mass and oxygen consumption holds across life history stages (neonate to adult) and sexes (Sims 1996), although the existence of sex-specific metabolic rates has not been investigated in this species, or to our knowledge, in elasmobranchs generally. Similarly, there is currently no evidence for metabolic temperature compensation in elasmobranchs (e.g., Tullis and Baillie 2005). Therefore, this oxygen consumption–body mass relationship was used to estimate standard metabolic rates, which were temperature-corrected using the Q_{10} value for *S. canicula* (Butler and Taylor 1975) of 2.16 determined between 7° and 17°C, and the Q_{10} metabolic rate conversion equation given in Davenport and Sayer (1993).

The model incorporates the energy expenditure attributable to activity (active metabolism, R_A). As with the energetic model of Sims et al. (2006), vertical depth

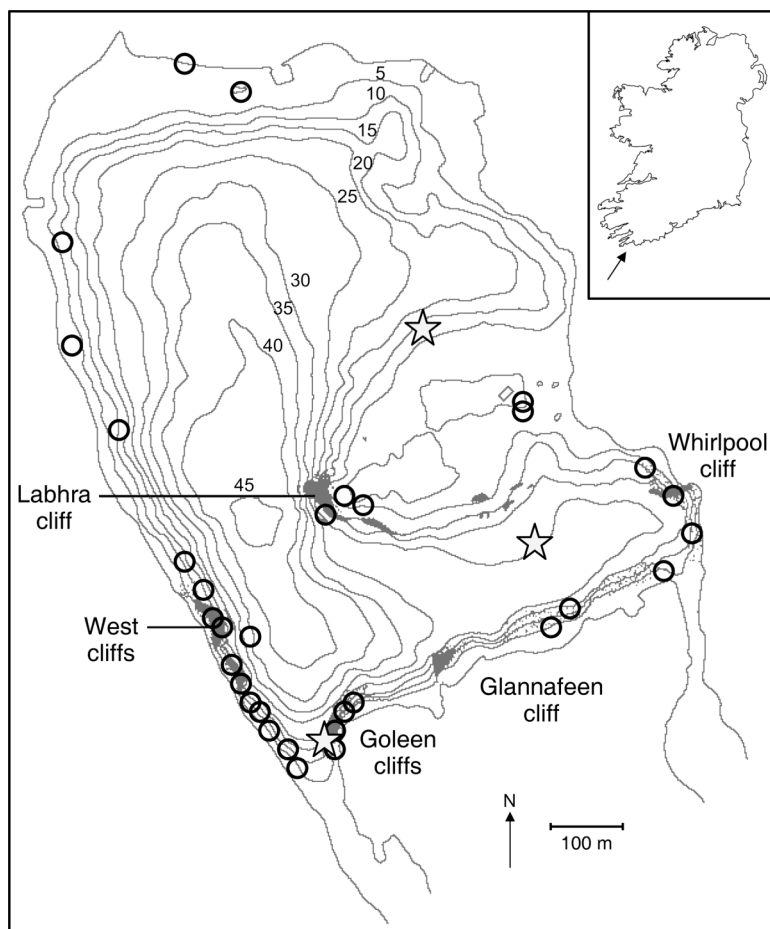


FIG. 1. Bathymetric chart indicating female-only refuge locations for the small-spotted catshark, *Scyliorhinus canicula*. The map of Lough Hyne, southwest Republic of Ireland, shows the distribution of boulder cliff habitats (gray-stippled areas) and sites used as female refuges between 1995 and 2005 (circles) (update of Sims [2005] and Sims et al. [2005]), as well as deployment locations of VR2 receivers (stars) in the north basin (top), south basin (middle), and outside the G1 female refuge (bottom). The base bathymetry map, with contour values in meters, was provided by I. Parnum and J. Turner of Bangor University.

changes were characterized into activity levels: “low” (vertical depth change of 0.1 to 0.9 m/10 min), “medium” (2.0 to 4.9 m/10 min), and “high” (>5.0 m/10 min). Oxygen consumption measurements of adult catsharks exhibiting low, medium, and high levels of swimming activity (Sims 1994) were then applied to the change in depth data. These 10-min estimates of active metabolic rate were temperature-corrected, as described previously, before subtracting the rates of standard metabolism.

Feeding metabolism (R_F) was also incorporated into the model. As with the model of Sims et al. (2006), it was assumed that catsharks captured prey items of mass equivalent to 6.5% of the catshark’s mass at a rate of one prey item every three nights. For adult catsharks (mass ~800 g) at 15°C, the relationship between specific dynamic action (SDA) and time can be described by the linear regression ($r^2 = 0.80$) given in Sims and Davies (1994):

$$VO_2 = -1.0128t + 135.61$$

where VO_2 is oxygen consumption in mg O_2 /h and t is time in hours. This relationship was used to determine the activity-free energy expenditure attributable to food consumption and digestion for each 10-min interval for 90 h following consumption of the prey item, this period being the SDA duration for a 6.5% of body mass meal (Sims 1994). Once again, metabolic rates were temperature-corrected according to the water temperature experienced by the fish at each time interval, minus the standard metabolic rate.

Direct observation

The movements of catsharks outside the G1 refuge were monitored through direct observation from a small moored boat. Most entrances of G1 were located between 1 and 4 m depth, enabling surface observations to be made without disturbance. Observations covering the 24-h period were spread over the course of each 2-

week field visit (total 210 h of observation). Low-light narrow-beam underwater torches (Underwater Kinetics, Poway, California, USA) were used for partial illumination during nocturnal observations. During October 2003, two underwater video cameras (Seacam low-light monochrome cameras with frame integration, varifocal lenses, and integral LED lighting; Rovtech System, Barrow in Furness, UK), connected to a digital video multiplexer (VDGHD16/e, Vista, UK), were deployed outside entrances to G1 to record the activity and behavior of passing male and female catsharks. The footage obtained (total 48 h) was later viewed using Wavereader software (Vista, Berkshire, UK).

In addition, the location within the lough of all grey seals (*Halichoerus grypus*) observed and their behavior (they are potential catshark predators) were noted during the normal course of research. As research activities were very similar throughout the two-year period of research, sighting effort was consistent across days and between trips.

Female catshark fecundity

Female catsharks caught during routine gill-netting were assessed noninvasively (external examination) for the presence of well-developed eggs in the oviducts. The seasonal percentage of gravid females was compared to simultaneous logged measurements of water temperature at G1 (Minilog, Vemco, Canada). In addition, the relationship between the number of eggs recovered from laboratory-kept females and aquaria water temperatures was investigated using segmented linear regression (SegReg 1.6.0.0, *available online*).⁸ This program applies multiple linear regressions to a data set by introducing breakpoints and performing separate linear regression analyses on the isolated segments (Oosterbaan 1994). The breakpoint is unknown and an iterative process is used to test multiple data fits. The selected function type ($n = 7$) is one that maximizes the coefficient of explanation to derive a significant breakpoint ($\alpha = 0.05$).

Video tracking procedures during laboratory experiments

Catshark behavior was monitored in the laboratory to examine the baseline behavior of the sexes under controlled conditions as well as their response to specific stimuli (i.e., conspecific/predator presence and increased temperature) during experimental trials. The behavior of male and female catsharks was monitored by tracking the movements of individual fish using a computer-aided video tracking system. Catshark movements within behavioral arenas (660-L capacity rectangular aquaria) were tracked using two ceiling-mounted color cameras (VCC-6572P, Sanyo, Osaka, Japan) linked to a PC running EthoVision Color Pro version 3.0 (Noldus, Wageningen, The Netherlands) video tracking software. Individuals were color-marked (65 mm dorsally mounted colored discs; for attachment procedures, see Sims et

al. 2006) and their movements were tracked in real time based on the color properties of the attached tags: the pixel position (X, Y coordinate) of the tag's center point was recorded at a sampling rate of 2.5 positions per second. During experimental trials, light levels were adjusted from "light" (~ 260 lux) during daylight hours to "twilight" (~ 35 lux) at night, where times of sunrise and sunset were determined from a nautical almanac.

Baseline activity patterns of the sexes

The movements of eight individual male and eight individual female catsharks were monitored in the laboratory prior to any choice experiments to quantify the effects on behavior of being held in groups or singly. The movements of these 16 "focal" fish were tracked for three days within each of two density treatments: either alone, or with three other same-sex fish. Order of density testing was assigned randomly across trials. Tracks were filtered for erroneous positions and a mixed-model ANOVA (MINITAB) was used to determine whether fish (random effect) and the fixed effects of sex, density, or time of day influenced the $\log(x + 1)$ -transformed mean rate of movement in day and nighttime windows.

The influence of predator presence on catshark behavior

The grey seal, *Halichoerus grypus*, the nursehound, *Scyliorhinus stellaris*, and the thornback ray, *Raja clavata*, are the only potential predators of small-spotted catsharks found in the Lough Hyne study site (Minchin 1987). Due to the size relationships between predator and prey, the grey seal is the only one of these likely to pose a predatory threat to adult catsharks. To determine whether the threat of seal predation influences catshark behavior, the movements of individual male and female catsharks were tracked during playback of grey seal underwater vocalizations, the frequency range of which were within the hearing range of the catsharks (Dijkgraaf 1963). Call sequences were constructed by splicing individual calls, obtained from the Bird and Mammal Sound Communication group at the University of St. Andrews (McCulloch 1999), into 12 2-min call sequences using 2-s segments of background noise (Cool Edit LE, Syntrillium Software, Phoenix, Arizona, USA). Control sequences were also constructed, in which individual calls in each call sequence were replaced by sections of triangular noise of base frequency 250 Hz, modulating by 100 Hz every 2 Hz. Sequences were played via an underwater speaker (Mark II 15–100 sound projector, Fish Guidance Systems, Winchester, UK). To avoid startle responses caused by the sudden onset of noise, volume was slowly faded in and out over 30 s of background noise. Each matched call and control sequence, where order of testing was allocated randomly and sequences were separated by a 2-min silence, was played to laboratory-kept male and female catsharks (four individuals per single-sex arena) at random times over a 48-h test period.

⁸ <http://www.waterlog.info/segreg.htm>

Catshark movements were video tracked throughout the test period and mean rate of movement determined for the 2-min period immediately prior to playback and the 2-min period during playback of the call sequence. To avoid pseudoreplication, responses to each of the 12 sequence pairs were averaged across fish of each sex. A Wilcoxon matched-pairs signed-ranks test (MINITAB) was used to compare the mean response of the sexes during call sequences to the mean activity level pre-playback, as well as to test for significant differences in response to call and control sequences.

The influence of male presence on female thermal habitat selection

Thermal choice chambers were used to investigate whether male presence influenced female thermal habitat selection. Experimental arenas were divided in half by a thick Perspex sheet with a bottom-located hole (0.2 m diameter \times 0.1 m height). Two female catsharks were placed into each of four arenas and the movements of all eight fish were video tracked. Fish were fed each day in the outflow chamber of each arena to condition the fish to occupy this compartment. Once a preference for the outflow chamber was established (a period of 10 days), a temperature gradient was imposed using a water heater (200-W aquarium heater, Clear-Seal, Birmingham, UK) to warm the water of the outflow chamber. This heater raised the temperature in the outflow chamber of the arena higher than that of the inflow, which received a constant input of chilled, filtered sea water (temperature difference $0.33^\circ \pm 0.63^\circ\text{C}$, mean \pm SD). Water temperatures were recorded every 15 minutes using temperature sensors with accuracy $\pm 1^\circ\text{C}$ from -30°C to 70°C and resolution 0.5°C (Thermochron iButton DS1921G, Dallas Semiconductor, Dallas, Texas, USA). After 6 days of continuous tracking under heterothermal conditions, two male fish were introduced into each arena and the movements of the female fish were tracked for a further 6 days. The temperature in the outflow chamber of the arena was then raised again, with the placement of an additional heater (300-W aquarium heater, Rena Cal, Annecy, France). During this second heterothermal treatment, the mean temperature difference between the two chambers was increased to 0.5°C (SD 1.20°C) and the movements of the female fish were tracked for a further 6 days.

Mean time spent in the outflow chamber was examined using Wilcoxon matched-pairs signed-ranks test (MINITAB). Directional tests were used because it was predicted that females should (1) decrease their use of the warm chamber of the arena with the onset of heterothermal conditions, (2) increase use of the warm chamber when males were added if the cost of male presence exceeded those incurred from higher temperatures, but (3) decrease use of this chamber as the temperature gradient increased, if this increase was sufficient to meet or exceed the costs of increased exposure to higher temperatures.

RESULTS

Activity patterns of free-ranging and laboratory-kept catsharks

Five archival tags were recovered (three male, two female) after times at liberty of up to 385 days (total 998 track days). These data sets revealed a predominant diel rhythm of increased nocturnal activity (Fig. 2a, b). However, temporally persistent (year-round) sex differences in activity patterns were also observed: females remained inactive during daylight hours and the length of activity bouts was constrained to the length of the dark period, which varied seasonally in this northern hemisphere temperate location (Fig. 2a, b). In contrast, male activity bouts were not restricted to the dark phase and all male fish were frequently active during daylight hours. As a result, the mean activity rate of the males was significantly greater than that of the females during the summer months at least. For example, the mean activity rate of the males exceeded that of the females by almost 2.3 times over the 10-day period from midday on 6 July to midday on 16 July 2003 ($F_{1,4} = 17.72$, $P = 0.024$).

In the laboratory, the movements of eight individual male and female fish, held both individually and together with three other same-sex fish between July and September 2003, revealed a significant influence of time of day on activity rates (elevated nocturnal activity; $F_{1,14} = 9.48$, $P = 0.008$), but no sex difference ($F_{1,14} = 0.01$, $P = 0.929$), density effect ($F_{1,14} = 0.34$, $P = 0.571$), or any interactions (all $P > 0.624$) were detected.

Habitat segregation of free-ranging catsharks

Examination of the fine-scale depth data revealed vertical habitat segregation of the sexes (Fig. 2b). Combined with spatial tracking (2551 track days; $n = 10$) and direct observation, these data showed that females aggregated and remained stationary in shallow water (~ 3.2 m) refuges during daylight hours (Fig. 2c) before moving into and remaining active in deeper water (~ 25 m) at night. In contrast, males generally spent daylight hours at depth (15–20 m), ascending to shallow waters (< 5 m) at dusk, and were then recorded to exploit a wide range of depths (1.1–23.4 m) nocturnally.

Spatial tracking of acoustic-tagged male catsharks (3473 track days; $n = 8$) showed that they remained within a relatively small core area (< 0.126 km²) for up to 94% of the time. However, all males moved outside core areas and to within at least 72 m of an acoustic receiver positioned directly outside the G1 female refuge at some point during tracking (tracking duration range 46–718 d; mean 434 d). Tagged males remained within the vicinity of G1 for up to 4 h and this regular pattern of visitation persisted throughout the annual cycle (Fig. 3a, b). These movements frequently coincided with the times of dawn and dusk (Fig. 3c).

Direct observation of wild catshark behavior

Surface observations revealed up to 15 females leaving G1 each night. Directed movements of males toward G1

were observed at all times of the day and night, but were more frequent at dusk and soon after dawn (Fig. 4). Males observed outside G1 at these times were seen to search seaweed-covered crevices. Although some males were observed to enter and exit the refuge (underwater video frames; Fig. 5), no males were ever seen in the refuge during underwater (SCUBA) surveys. Returning females were often closely followed by males and mating attempts were documented, which females evaded by swimming quickly into the refuge. Male–female interactions were also evident, usually comprising one male chasing another from the vicinity of G1.

Thermal habitat selection and energy modeling

Archival tag data revealed that although the average daily temperature exposure of male catsharks peaked at 16.9°C during August, daytime refuging in shallow water exposed females to temperatures above this level for up to 75% of the time throughout the same month (refuging temperature range 14.3–18.1°C for female 1 and 14.5–18.4°C for female 2; maximum mean daily temperature exposure 17.6°C). However, an empirical model of metabolism for actual thermal habitats occupied by each wild fish indicated that average estimated daily energy costs were similar between the sexes (39.3–56.0 kJ for females and 41.9–58.4 kJ for males; see Table 2).

Egg production rates

An inverse relationship was found between the presence of well-developed eggs in the oviducts of free-ranging catsharks and ambient temperature outside the G1 refuge (Fig. 6a). The percentage of egg-bearing females decreased from 80% to 40% between winter and summer, while mean daily refuge temperatures concomitantly rose from 9.5° to 15.3°C. A negative relationship was also found between egg production rates of laboratory-held fish and aquaria water temperature (Fig. 6b). Segmented linear regression analysis revealed a significant breakpoint in the data at 17.72°C, above which the number of eggs recovered from individual laboratory females was very low or zero (0.02 ± 0.03 eggs·fish⁻¹·d⁻¹, mean \pm SD). At lower temperatures below this threshold, egg production was higher and more variable (up to 0.32 ± 0.09 eggs·fish⁻¹·d⁻¹).

Influence of predator presence on catshark behavior

The sightings of grey seals in Lough Hyne followed a seasonal pattern. Grey seal sightings were most frequent during winter (5–6 individuals per day), and it was only at this time of year that sightings of more than one individual were observed (up to three individuals in a group). No seals were observed during summer field visits, and only low numbers were observed in spring and autumn (0–1.06 individuals per day).

Median activity levels of both male and female catsharks appeared to be slightly higher during playback of seal vocalization (call) sequences (1.07 ± 2.8 and 2.62

± 2.4 cm/s; median \pm SD) than pre-playback (0.02 ± 0.8 and 2.60 ± 2.1 cm/s for male and female catsharks, respectively). However, rates of movement during playback of call sequences did not differ significantly from normal levels: for males, the median increase in activity was 0.94 cm/s (Wilcoxon statistic = 8.0, $n = 10$, $P = 0.053$); for females, the median increase in activity was 0.25 cm/s (Wilcoxon statistic = 23.0, $n = 11$, $P = 0.398$). In addition, responses to call and control sequences (median activity level 0.94 ± 1.7 cm/s for males, 4.22 ± 2.1 cm/s for females) did not differ significantly: for males, median difference was 0.30 cm/s (Wilcoxon statistic = 39.0, $n = 10$, $P = 0.262$); for females, median difference was 0.89 cm/s (Wilcoxon statistic = 60.0, $n = 12$, $P = 0.108$).

The influence of male presence on female thermal habitat selection

Female preference for the compartment in which food was made available was overridden by temperature; female preference shifted to the cool, food-free chamber when a thermal gradient was introduced; mean hours spent in the outflow decreased from 14.8 to 3.9 h/d (Wilcoxon statistic = 0.0, $n = 8$, $P = 0.007$; Fig. 7). When males were introduced to the experimental arenas, females increased the amount of time spent in the warm chamber (mean 5.6 h/d spent in outflow; Wilcoxon statistic = 31.0, $n = 8$, $P = 0.040$). However, further increase (+0.2°C) in the temperature gradient resulted in female preference reverting to the cooler chamber (mean 2.6 h/d spent in outflow; Wilcoxon statistic = 3.0, $n = 8$, $P = 0.021$).

DISCUSSION

In promiscuous species, the evolutionary interests of the two sexes are likely to differ with regard to mating (Parker 2006). The resulting sexual conflict in mating systems provides a potential mechanism for sexual segregation as females strive to evade males and unwanted matings. However, although social factors are recognized as potential drivers of sexual segregation (social factors hypothesis; Conradt 2005, Ruckstuhl and Clutton-Brock 2005, Wearmouth and Sims 2008), they have received little empirical support. This is primarily due to the fact that the majority of species investigated (typically ungulates) exhibit sexual size dimorphism and thus sex differences in attributes such as nutritional requirements, activity budgets, or predation risk provide a better explanation for sex differences in habitat selection. Here we explored the underlying causes for sexual segregation in the sexually monomorphic lesser spotted catshark, *S. canicula*, using a combination of long-term acoustic and archival tracking of wild individuals and direct observation of male–male and male–female interactions in the field, together with complementary, hypothesis-driven laboratory experiments. The aim of this research was to explore the suitability of multiple hypotheses that have been forwarded to account for sexual segregation. Given the

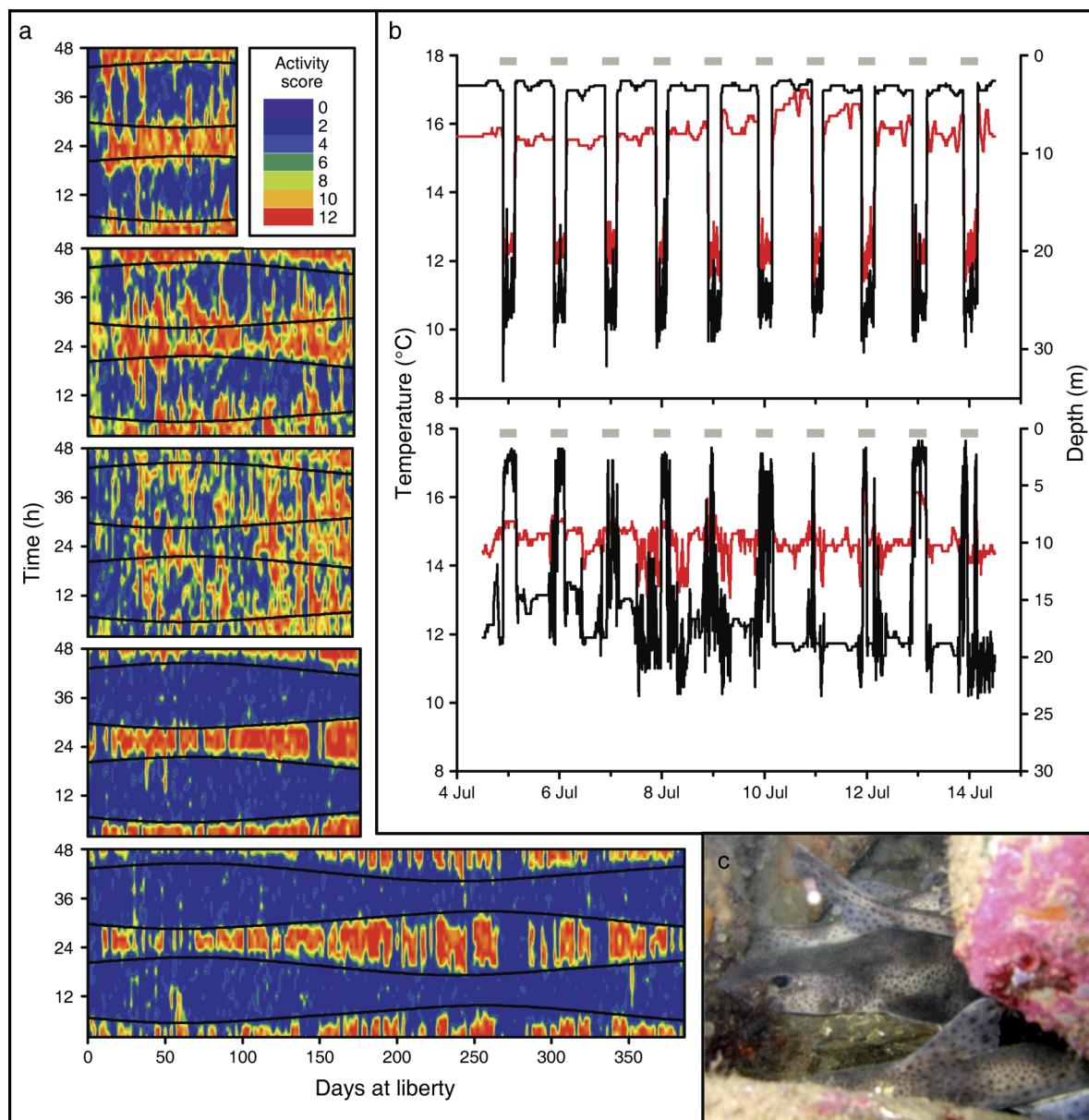


FIG. 2. Long-term sex differences in catshark behavior and habitat. (a) Activity patterns of (from top) males 1, 2, and 3 and females 1 and 2 between April 2003 and April 2004. Each fish's activity record is shown as a double-plot actogram, with 2-h summed binary activity scores, ranging from 0 (inactive) to 12 (most active), over 48 h on the x-axis and days at liberty on the y-axis. Black lines indicate the times of sunrise and sunset as determined from a nautical almanac. (b) Examples of the 10-day temperature (red) and depth (black) record for female 1 (top) and male 2 (bottom) in July 2003. Short gray horizontal bars indicate dark periods. (c) Four female catsharks refuging in G1.

documented aggressive nature of shark courtship and mating, in particular we investigated whether female-only refuging behavior functions to reduce levels of male harassment to individual females and thus may be a principal driver of sexual segregation in this species (social aversion hypothesis).

Elasmobranch courtship and mating involves a prolonged series of complex behaviors. Single females may be pursued by multiple males and incur significant injuries during courtship and mating, as the male will

often bite the female to subjugate her (Klimley 1980). In *S. canicula*, the male grasps the female's pectoral fin in his teeth and wrestles her in an attempt to manipulate her into position for mating (Schmidtlein 1878). As a result, wild-caught females frequently bear significant scars and teeth marks on their fins (Fig. 8a). Male *S. canicula* carry sperm reserves year-round (Garnier et al. 1999), indicating a protracted mating season in this species. However, females are known to store active sperm within the nidamentary, or shell-producing,

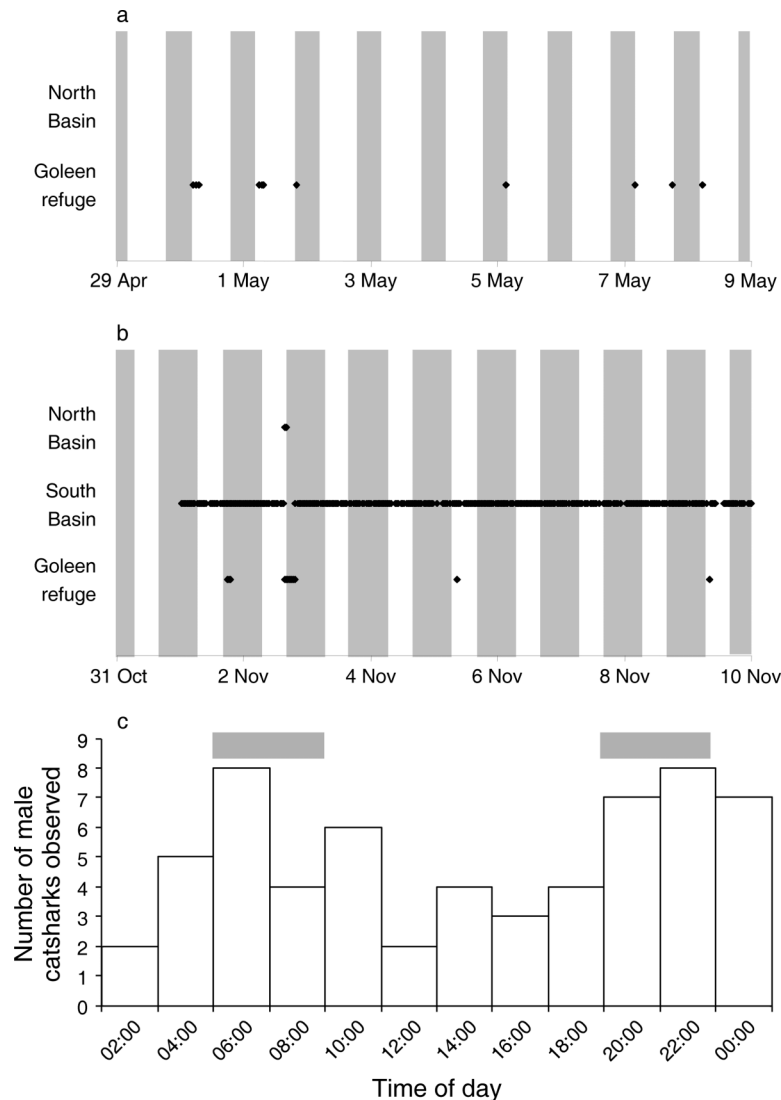


FIG. 3. Examples of long-term tracked male catsharks visiting the female refuge (G1) at dawn and dusk. For (a) male 1 during spring 2003 and (b) male 2 during autumn 2003, black horizontal diamonds show a 10-day record of detections by VR2 receivers in the north basin (top), south basin (middle, if present), and the G1 (Goleen) refuge (bottom); vertical gray columns indicate dark periods. (c) Frequency histogram showing timings over 24 h of male detections on the VR2 receiver at the G1 female refuge where males remained in the area for 10–240 min. The two horizontal gray bars indicate sunrise and sunset periods, respectively.

gland: sperm are secreted alongside the albumen and egg case, ensuring fertilization of every egg produced (Metten 1939a, b). Laboratory-kept female *S. canicula*, maintained in isolation from males, have been observed to produce fertile eggs for periods up to at least 260 days (Griffiths et al. 2012), and a closely related species, the chain catshark, *S. retifer*, has been recorded to produce viable eggs after 843 days in isolation (Castro et al. 1988).

Because female *S. canicula* are capable of storing viable sperm for long periods of time (months) and therefore copulation need not precede every ovulation in this species, we hypothesized that sexual segregation may provide female catsharks with a means of avoiding

potential injury during what might be unsolicited mating attempts. One prediction of this hypothesis is that sexual segregation, like mating activity, should occur year-round. Electronic tracking and direct observation of free-ranging catsharks revealed sex differences in activity patterns and vertical habitat segregation. Male fish were frequently active during the day, spending daylight hours at depth (15–20 m), ascending to shallow waters (<5 m) at dusk, and then exploiting a wide range of depths (1.1–23.4 m) nocturnally. In contrast, females aggregated and remained stationary in shallow (~3.2 m) water refuges during daylight hours before moving into and remaining active in deeper water (~25 m) at night. These sex differences in activity patterns and vertical

habitat segregation reflect those previously described by Sims et al. (2001), but here were shown to be temporally persistent: female occupation of shallow-water refuges occurred year-round.

Sex-specific activity patterns are predicted under the activity budget hypothesis. It is assumed that sexual dimorphism in body size and/or sex differences in reproductive investment underlie these alternate activity patterns and manifest as disparities in the amount of time the sexes allocate to activities such as foraging for resources and resting. As a result, mixed-sex groups experience high fission rates, which ultimately lead to segregation of the sexes as the species separates into single-sex groups composed of individuals with similar activity budgets. *S. canicula* is sexually monomorphic with respect to body size, forages solitarily, is oviparous, and does not exhibit parental care, with egg cases being laid and anchored to macroalgae in shallow-water habitats (Ellis and Shackley 1997). Therefore, it seems unlikely that inherent sex differences in activity underlie the alternate activity patterns demonstrated here. This observation is supported by the breakdown of sex differences in activity patterns when individuals were housed under controlled conditions (in the laboratory), which in turn suggests that the activity budget hypothesis cannot reasonably explain sexual segregation in this species.

Body size dimorphism and parental care for vulnerable offspring also underlie the predation risk hypothesis. Under this hypothesis it is assumed that one sex (generally the female) is more at risk to predation than the other sex and it is therefore predicted that the more susceptible sex occupies “safer” habitats to avoid predation. That one sex should be more susceptible to predation is difficult to understand in a species that is sexually monomorphic with respect to body size and does not exhibit parental care. Moreover, it is unclear whether *S. canicula* is subject to any major threat of predation at the study site; although grey seals are frequently observed foraging for teleost fish in Lough Hyne, there is no evidence from either scat analysis or direct observation that they consume catsharks at this site (Wearmouth 2006). Grey seals were seasonal visitors to the lough, being sighted regularly during winter months, but absent in summer, and yet female catsharks refuged year-round. Furthermore, in the laboratory, male and female catsharks failed to exhibit an obvious movement response to the aural presence of seals (a proxy for increased predation risk), which, coupled with the fact that the incidence of female refuge use did not reflect the potential risk of seal predation, suggests that the predation risk hypothesis is unlikely to account fully for sexual segregation in this species.

The use of shallow, warmer water refuges by females may have significant thermal consequences because body temperature, which in ectotherms is governed by ambient temperature, influences many aspects of animal biology, including activity, metabolism, egg production,

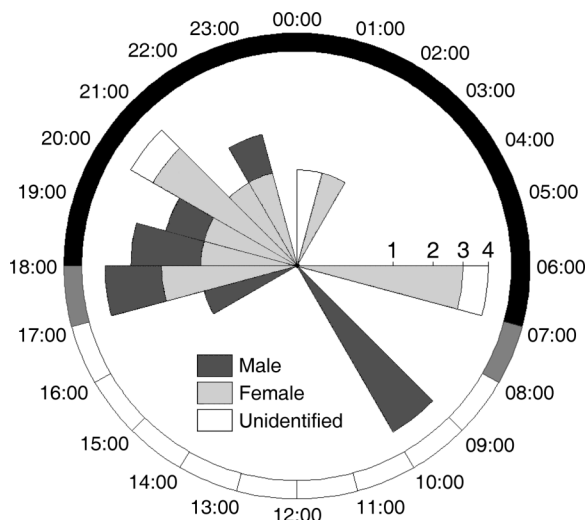


FIG. 4. Male sharks synchronize their presence at refuges with female emergence/return. Radiating segments show the number of male (dark gray), female (light gray), and sex unknown (open) catsharks seen outside the G1 refuge during October 2004 over the 24-h cycle. The size of each segment is area-scaled to the number of individuals observed, as indicated by the numbers along the 06:00 hours axis. On the perimeter, the black band indicates the dark period, and the gray bands indicate the times of dawn and dusk.

and growth. However, although the average daily temperature exposure of female catsharks exceeded that of males for up to 75% of the time, energy expenditure modeling indicated that average daily costs were similar between the sexes. This suggests that female catsharks were able to compensate for the effects of higher temperature-induced metabolic rate on daily costs by remaining inactive while refuging, thereby reducing the active (and largest) component of metabolic cost. Nonetheless, female egg production did appear to be affected by exposure to the highest temperatures recorded in refuges, because egg production rates were reduced when water temperatures were warmest. During summer months, wild female catsharks refuging in shallow-water caves were regularly exposed to temperatures above the laboratory-observed threshold temperature (for 18.7% and 15.7% of the time during August for females 1 and 2, respectively). This could explain the observed decrease in summer egg production. Although sea water temperatures are intrinsically linked to time of year, females in Lough Hyne continued to produce eggs during summer months, albeit at a reduced level. Although fecundity of the wild female population is reduced by refuging, the formation of female-only aggregations in refuges was not abandoned as a behavioral strategy when water temperatures peaked. Because the selection of sex-specific thermal habitats at which fecundity (and thereby reproductive success) is maximized is central to the thermal niche-fecundity hypothesis, the observation that occupation of shallow, warm-water caves appears to lower female fecundity

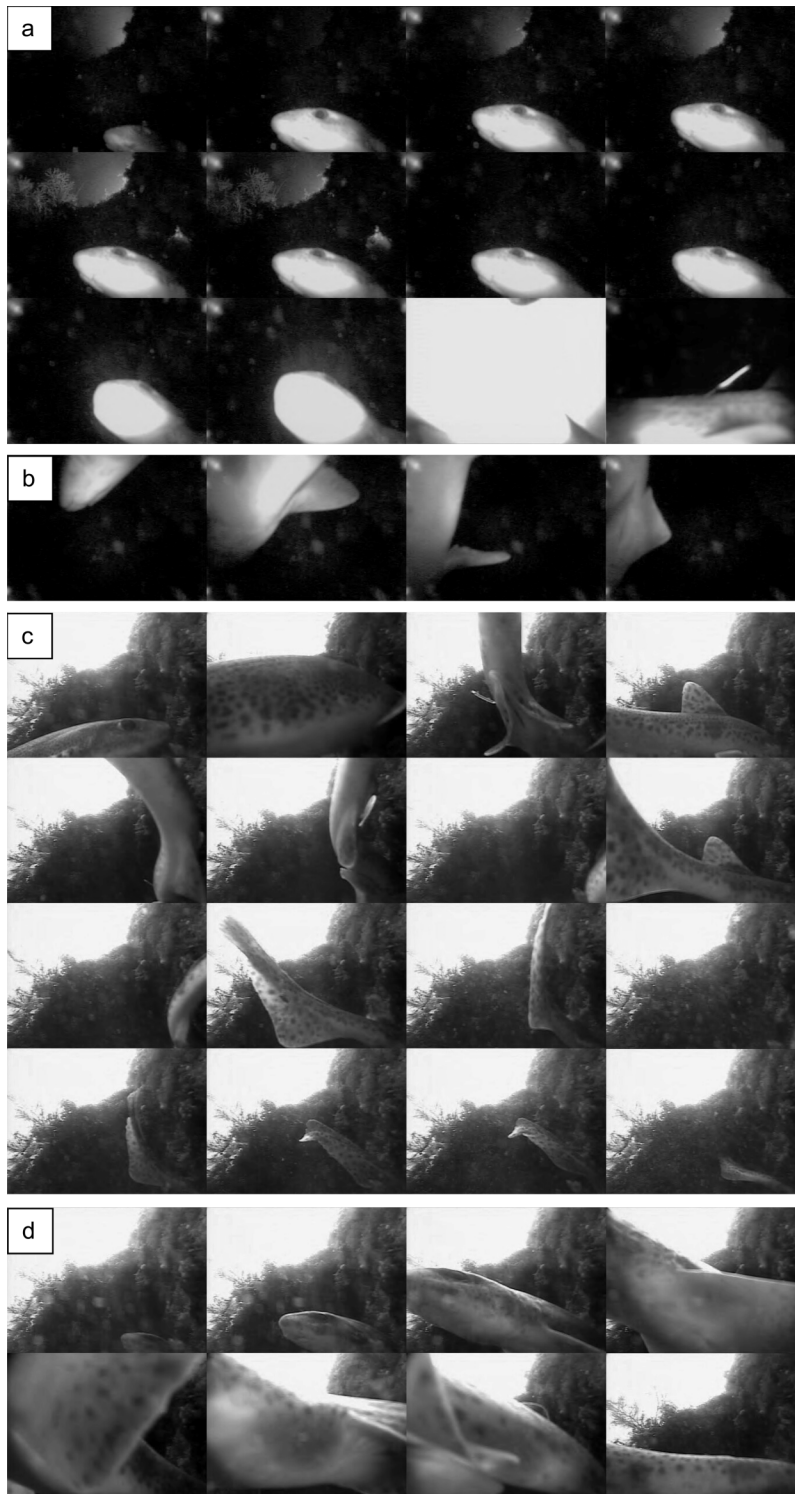


FIG. 5. Direct observations of catshark refuging behavior at G1. Underwater video observations outside a female refuge entrance showing: (a) female catshark (determined by snout shape) exiting the refuge at dusk (1 frame/s); (b) female catshark (lack of claspers in fourth frame) returning to the refuge at dawn (2 frames/s); (c) male catshark (claspers visible in third frame) entering the refuge mid-morning (1 frame/s); and (d) male catshark (claspers visible in seventh frame) exiting the refuge mid-morning (2 frames/s).

TABLE 2. Estimated energy expenditure of male and female small-spotted catsharks (*Scyliorhinus canicula*).

Month	Mean daily energy cost (kJ)					Female saving (%)	
	Female 1	Female 2	Male 2	Male 3	Male 1	Minimum	Maximum
May	41.902	39.289	43.995	41.897	43.775	-0.01	10.7
June	44.564	42.566	50.394	45.753	45.075	1.1	15.5
July	47.019	46.881	49.775	49.732	51.328	5.5	8.7
August	50.639	49.503	49.164	54.368		-3.0	8.9
September	50.839	48.155	54.254	58.111		6.3	17.1
October	56.031	51.434	57.061	58.426		1.8	12.0

Note: Energy expenditure of two females and three males was calculated by month between May and October 2003 for each individual, together with the range of energy savings estimated for refuging females, reflecting the efficiency of that female strategy in relation to expenditure estimated for the males. The minimum saving is the percentage difference between the most energetically expensive female strategy and the least expensive male strategy, and vice versa for the maximum saving.

during summer months suggests that this hypothesis in itself cannot explain the pattern of sexual segregation observed in this species.

That female catsharks refuge year-round, despite the cost of refuge occupation in terms of reduced fecundity, raises the question of whether this behavior provides a

true refuge from male mating attempts. The G1 refuge was a prominent rockfall comprising a complex of multiple entrances and chambers housing aggregating females. All 32 refuges that have been identified at the study site to date are located in shallow water, reflecting the availability of steep, rocky-cliff habitats (see Fig. 1). Males were shown to move away from their core areas and visit the G1 refuge at the times when they would be most likely to encounter females emerging from (at dusk) or returning to (at dawn) the refuge; they also attempted to mate with the emerging or returning females. These observations, coupled with sightings of females evading mating attempts by entering the refuge, are consistent with the hypothesis of female avoidance

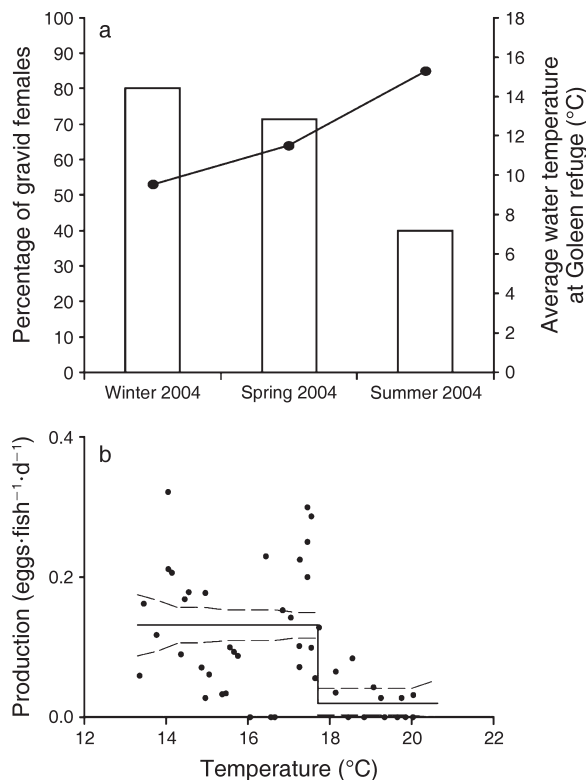


FIG. 6. Increasing water temperature decreases egg production. (a) The percentage of females carrying well-developed eggs (vertical bars) during winter (January), spring (April), and summer (July) 2004, together with the average water temperatures (black line) measured at G1 over the same period. (b) Egg production under controlled conditions in relation to temperature. Segmented regression analysis of the relationship between the number of eggs laid per fish per day and the temperature of the female aquaria reveals a significant breakpoint at the threshold temperature of 17.7°C, with lower production at high temperatures. The dashed lines represent 95% confidence levels.

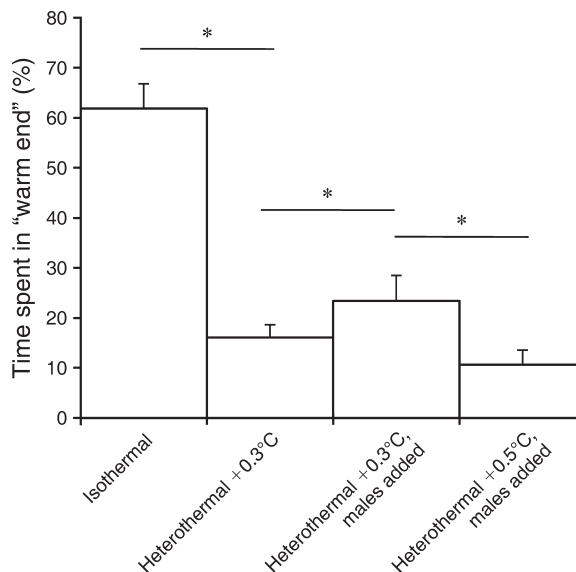


FIG. 7. Percentage of the time (mean + SE) that females spent in the "warm" compartment of the arena, without males under isothermal conditions (0°C temperature gradient) and heterothermal conditions (0.3°C temperature gradient) vs. with males introduced under 0.3°C and 0.5°C temperature gradient treatments. The figure indicates that females pay to avoid males. The difference between mean time females spent in the warm compartment without and with males under heterothermal conditions (second and third histogram bars) was significant (Wilcoxon matched-pairs signed-ranks test).

* $P < 0.05$.



FIG. 8. Female refuge use to evade male mating activity appears to be geographically widespread. (a) Photograph of the dorsal fin region of a female catshark captured in Lough Hyne bearing an array of teeth marks that have contributed to significant damage to the trailing edge of the fin. These teeth marks are thought to be the result of male coercion during mating activity. (b) Female catsharks refuging in a boulder crevice in shallow water (~ 5 m depth) off the coast of Plymouth, UK (photo courtesy of K. Hiscock). In addition to southwest Ireland (Lough Hyne study site) and southwest England (Plymouth, $50^{\circ}21' \text{ N}$, $004^{\circ}09' \text{ W}$), female *S. canicula* refuging occurs in other locations, including northwest Scotland (Loch Melfort, $56^{\circ}15' \text{ N}$, $005^{\circ}31' \text{ W}$; D. W. Sims, *personal observation*) and north Wales (Menai Strait, $53^{\circ}17' \text{ N}$, $004^{\circ}02' \text{ W}$; M. Costello, *personal communication*).

behavior driving the observed population distribution. This suggests that these natural structures provide females with a true refuge from male harassment and copulation; indeed, the spatial confinement of the narrow chambers occupied by females within the refuge makes copulation physically impossible (Fig. 2c). Female behaviors that preclude mating have also been observed in green turtles (*Chelonia mydas*), nurse sharks (*Ginglymostoma cirratum*), and whitetip reef sharks (*Triaenodon obesus*). Unreceptive green turtles occupy female-only lagoons and will prevent males from mating by folding their hind flippers, directly confronting their pursuers, or by entering water too shallow for mating to take place (Booth and Peters 1972). The latter strategy is

also adopted by the female nurse shark (Carrier et al. 1994), whereas the female whitetip reef shark will attempt to maintain her ventral surface to the substrate, thereby limiting access to her cloaca (Whitney et al. 2004). These behaviors are analogous to the occupation of physically constricted refuges by female catsharks.

To test directly whether females did indeed avoid males, female habitat preferences were examined under heterothermal conditions without and with the presence of males. The results of this experiment indicate that, although females traded off food availability for thermal habitat selection, this relationship was influenced by male presence, as females spent more time in suboptimal thermal habitats when males were present. Hence, females were willing to pay in energy terms to avoid males. However, male presence only appeared to influence female habitat choice over a narrow temperature range, indicating that small increases in temperature (0.2°C) above an upper preference limit override the potential cost to females of male presence.

Overall, our results indicate year-round female avoidance of unwanted sexual activity from some males, which leads to sexual segregation through female occupation of refuge habitats that are suboptimal in terms of fecundity for ecologically relevant time periods. Refuge temperatures appear to be suboptimal for egg production for up to 19% of the time during summer months and probably contribute to the reduction in egg production seen in wild females at this time. This suggests that female catsharks trade egg production (fecundity) for control of mating and the costs associated with unwanted matings (e.g., injury). Because none of the alternative hypotheses investigated (activity budget hypothesis, predation risk hypothesis, thermal niche–fecundity hypothesis) could explain sufficiently the patterns of sexual segregation that we observed in this species, we conclude that the social factors (male avoidance) hypothesis provides the most parsimonious explanation of our field and laboratory empirical results for *S. canicula*.

Female avoidance of male sexual harassment is increasingly being cited as a potential driver of sexual segregation as the observation of this behavior has spread to species other than ungulates. For example, in addition to female green turtles, nurse sharks, and whitetip reef sharks, Galapagos sea lions (*Zalophus wollebaceki*), southern sea lions (*Otaria byronia*), river dolphins (*Inia geoffrensis*), red-sided garter snakes (*Thamnophis sirtalis parietalis*), guppies (*Poecilia reticulata*), and the Wellington tree weta (*Hemideina crassidens*), have all been suggested to segregate from males and/or to adopt behaviors to avoid male harassment (Campagna et al. 1992, Shine et al. 2000, Martin and da Silva 2004, Wolf et al. 2005, Kelly 2006, Darden and Croft 2008). However, despite the increasingly frequent citing of male avoidance as a potential driver for sexual segregation, there generally has been a lack of an experimental approach to test hypotheses

about wild observations, and few consider multiple hypotheses within a single study. In this study we have examined multiple hypotheses to investigate the underlying mechanism for sexual segregation in a sexually monomorphic study species. To our knowledge, we have provided the first empirical evidence for female avoidance of male harassment as an underlying cause of long-term sexual segregation in a wild vertebrate population.

Our results demonstrate how sexual conflict in mating strategy can influence the spatial structuring and dynamics of a vertebrate population. Female-only refugia appears to be geographically widespread in *S. canicula*. It is not limited to the site that we studied, but has now been documented in several open-coast locations, including in the Western English Channel (for photograph, see Fig. 8b). Male avoidance by choosy females may, therefore, have wider implications for many species that also exhibit sexual segregation (Wearmouth and Sims 2008), including the conservation of vulnerable species. For example, worldwide declines in shark populations due to overfishing may be exacerbated by the effects of area-focused fisheries on sexually segregating species (Mucientes et al. 2009). Female aggregation in specific habitats could expose mature females, including those pregnant, to higher risk of capture by area-focused fisheries. Thus, long-term sexual segregation driven by female avoidance of males, as demonstrated here, may have far-reaching ecological and evolutionary implications through its influence on the social structure and productivity of populations.

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SUPPLEMENTAL MATERIAL

Data Availability

Data associated with this paper have been deposited in Dryad: <http://dx.doi.org/10.5061/dryad.5f4d8>