

Research article

Open Access

Female philopatry in a heterogeneous environment: ordinary conditions leading to extraordinary ESS sex ratios

Vincent Hulin* and Jean-Michel Guillon

Address: Univ Paris-Sud, CNRS, AgroParisTech, Laboratoire Ecologie, Systématique et Evolution, UMR 8079, Bâtiment 362, Orsay, F-91405, France

Email: Vincent Hulin* - vincent.hulin@u-psud.fr; Jean-Michel Guillon - jean-michel.guillon@u-psud.fr

* Corresponding author

Published: 6 February 2007

Received: 26 October 2006

BMC Evolutionary Biology 2007, **7**:13 doi:10.1186/1471-2148-7-13

Accepted: 6 February 2007

This article is available from: <http://www.biomedcentral.com/1471-2148/7/13>

© 2007 Hulin and Guillon; licensee BioMed Central Ltd.

This is an Open Access article distributed under the terms of the Creative Commons Attribution License (<http://creativecommons.org/licenses/by/2.0>), which permits unrestricted use, distribution, and reproduction in any medium, provided the original work is properly cited.

Abstract

Background: We use a simulation-based model to study the impact of female philopatry and heterogeneity of habitat quality on the evolution of primary sex ratio.

Results: We show that these conditions may lead to strongly biased ESS habitat-dependent sex ratios, under two kinds of density-dependent population regulation. ESS sex ratios are always biased towards females in good habitats, towards males in poor habitats, and are generally equilibrated considering the whole population. Noticeably, the predicted bias of sex ratio usually increases with decreasing female philopatry.

Conclusion: The selection forces responsible for these results are fully described. This study provides a new perspective on the evolutionary significance of temperature sex determination. We discuss the case of turtles by comparing our theoretical results with field observations.

Background

Natal philopatry, i. e. the tendency for individuals to breed at or near their place of origin, has been described in a variety of animal species, including mammals [1], birds [reviewed in [2]], reptiles [3], and fish [4]. In such species, sex biased dispersal has often been observed as a result of natal homing being more frequent in one sex than in the other [5,6]. Indeed, there seems to be a tendency for female-biased dispersal in birds and male-biased dispersal in mammals [7-9].

Sex-biased dispersal has important consequences on the dynamics and on the social and genetic structures of natural populations [10,11], as well as on the evolution of phenotypic traits [12]. In particular, sex-biased dispersal provides the conditions for the evolution of biased sex ratios: parental manipulation of the sex ratio allows indi-

viduals to avoid kin competition [13,14], to benefit from local resource enhancement [15], or to select habitat in a heterogeneous environment [16].

Since its description, the determination of sex by temperature (TSD) in many reptiles has been a long standing puzzle from an evolutionary point of view [17-21]. The extreme sex ratios sometimes found in natural nests are indeed difficult to reconcile with the Fisherian frequency-dependent selection for equal investment in both sexes [22]. In order to find an adaptive explanation for environmental sex determination, Charnov and Bull [23] proposed a theoretical model in which habitat is heterogeneous and sexes benefit differentially from habitat quality. However, according to Warner and Shine [24], the assumptions of this model are difficult to test in rep-

tiles, and the published literature "reflects its overall plausibility [...] rather than specific experimental evidence".

One of the latest proposed hypotheses accounting for TSD in reptiles is based on female natal philopatry [16,25]. In sea turtles in particular, there is substantial evidence for natal homing of nesting females [26,27] and for the existence of male dispersal [28-30]. This has led to the hypothesis that nest site quality, if incubation success differs between nesting sites, could be inherited maternally [31]. Such spatial variability of incubation success is apparently frequent on nesting grounds [32-34].

According to Reinhold [25] and Julliard [16], sex-specific dispersal should lead to satisfy Charnov and Bull's [23] assumption that sexes benefit differentially from habitat quality. In a heterogeneous environment, natural selection should favour the sex ratio strategy maximizing the number of offspring breeding in high-quality habitats. Therefore, the evolutionary stable strategy (ESS) of sex ratio is one that overproduces the less dispersing sex (females in the case of female natal homing) in high-quality nesting sites and overproduces the most dispersing sex (males in the case of female natal homing) in low-quality nesting sites [16].

The model of Julliard [16] is based on several assumptions other than sex-biased dispersal and habitat patches of different quality. First, it assumes that reproduction, from mating to birth, occurs in the same patch. It also assumes that the population size is regulated by density-dependence occurring within each patch. These assumptions may be violated in migrating species, such as aquatic turtles that live in water and nest on earth. Because the scales at which mating and density-dependent regulation occur are key factors for population dynamics and evolution [35], we here present a new model introducing important modifications: mating sites are independent from nesting sites, and population regulation may occur either within nesting sites (hereafter named HABITAT model) or at the level of the whole population (TOTAL model). In any case, we show that the ESS primary sex ratio can be strongly biased depending on the nesting habitat but that the sex ratio of the overall population is generally equilibrated.

Results

The model

We use an individual-based simulation model to find the ESS primary sex ratio strategy dependent on habitat quality under female natal philopatry. The model describes a simplified life-cycle of sea turtles (fig. 1).

Nesting beach

The nesting beach is divided in 2 kinds of habitat differing in their quality: GOOD habitats (proportion g of the nest-

ing beach) or POOR habitats (proportion $1-g$), with $0 < g < 1$ (fig. 1). In GOOD habitats, a nesting female produces F times more offspring than in POOR habitats, with $F > 1$.

Sex ratio

We use a genetic architecture that allows the unconstrained evolution of sex ratio in each habitat so that the ESS is reached at the equilibrium. The strategy of sex ratio related to the habitat for every adult is determined by 2 alleles (G_1/G_2) the mean of which determines the offspring sex ratio (percentage of males) for nests in GOOD habitats, and 2 alleles (P_1/P_2) the mean of which determines the sex ratio for nests in POOR habitats, with G_1 , G_2 , P_1 and P_2 , between 0 and 1. These alleles are located on 2 unlinked loci so that any offspring independently inherits one allele of its mother (G_{mother} and P_{mother}) and one of its father (G_{father} and P_{father}) at each locus. At each generation, an allele has a probability 0.005 to mutate, and one mutation is an increase or decrease of 0.005 in the value of the allele.

Population

The population size is fixed equal to 5,000 adults. Each adult is defined by its sex (male or female), the kind of habitat where it was born (GOOD or POOR), and the values of G_1 , G_2 , P_1 and P_2 . Generations are discrete: adults breed once before dying. The sex ratio of the overall population (SR_{tot}) is defined as the total number of males divided by 5,000.

Reproduction and dispersal

Mating takes place in a unique reproductive area (fig. 1) where all adults meet, regardless of their provenance habitat. Each female mates with one randomly chosen male. Females then return to the beach to nest. A proportion $(1-d_f)$ of the females ('non-dispersing females') nest in the same kind of habitat where they were born. The complement (d_f) are considered as 'dispersing females' and are randomly distributed between GOOD and POOR habitats: for any dispersing female, the probability to nest in a GOOD habitat is g and in a POOR habitat is $(1-g)$.

Density-dependence regulation

We apply one of two different kinds of density-dependent regulation. The first one (called HABITAT) occurs in each habitat and corresponds to a regulation at the scale of the nesting beach: 5,000 individuals will grow to adulthood, a proportion $Fg/(Fg+1-g)$ born in GOOD habitats and a proportion $(1-g)/(Fg+1-g)$ born in POOR habitats. The second one (called TOTAL) consists in the random draw of 5,000 individuals in the entire population of offspring, which will grow into adulthood. Then, in the adult population, the proportions of individuals born in GOOD habitats and in POOR habitats are respectively $FN_g/(FN_g+N_p)$ and $N_p/(FN_g+N_p)$, with N_p and N_g the numbers of females

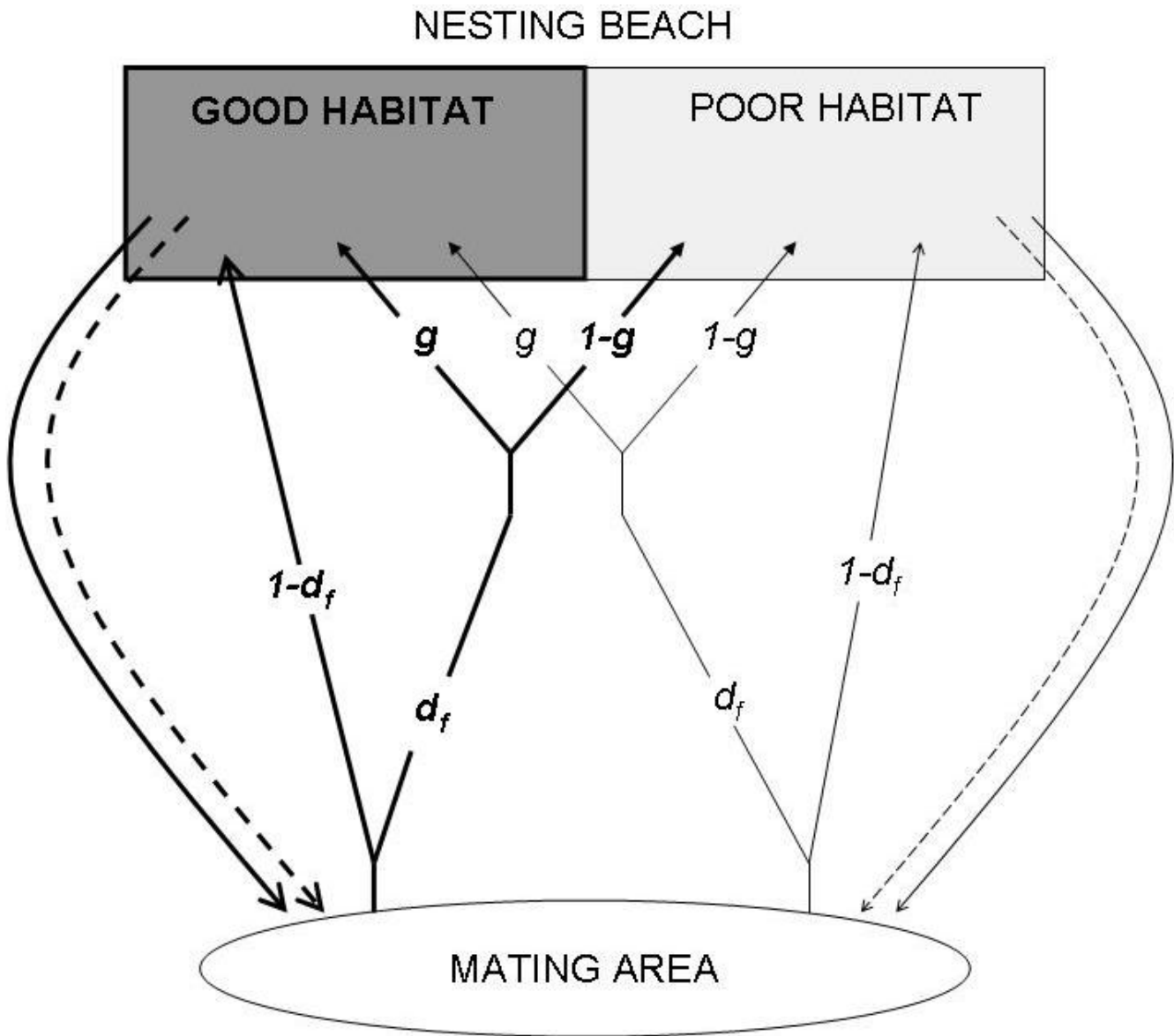


Figure 1
Simplified life-cycle used in the model. The parameters on the lines are the probability for an individual to follow it (equal to 1 in the absence of notation). Dashed lines are for males, plain lines for females. Bold lines represent individuals native from GOOD habitats, thin lines represent individuals native from POOR habitats.

nesting in POOR and GOOD habitats. This corresponds to a regulation at the scale of the entire population, on feeding grounds for example.

Simulation results

HABITAT density-dependent regulation (fig. 2)

For $d_f = 0$ (total philopatry), the ESS sex ratios are equilibrated in both habitats ($G = P = 0.5$). For $0 < d_f < 1$ (partial philopatry), the sex ratio is always biased towards males in the POOR habitat and towards females in the GOOD

habitat ($G < 0.5 < P$). For given values of F and d_f , the sex ratio is more biased in the habitat that contributes less to the whole population: when the proportion of females nesting in GOOD habitats is higher than the proportion of females nesting in POOR habitats ($Fg > 1-g$), the sex ratio is more biased in the POOR habitat; when $Fg < 1-g$, the sex ratio is more biased in the GOOD habitat. The sex ratio of the whole population is always unbiased ($SR_{tot} = 0.5$). When F or d_f increases, the habitat-dependent sex ratios are more and more biased, until the sex ratio in one

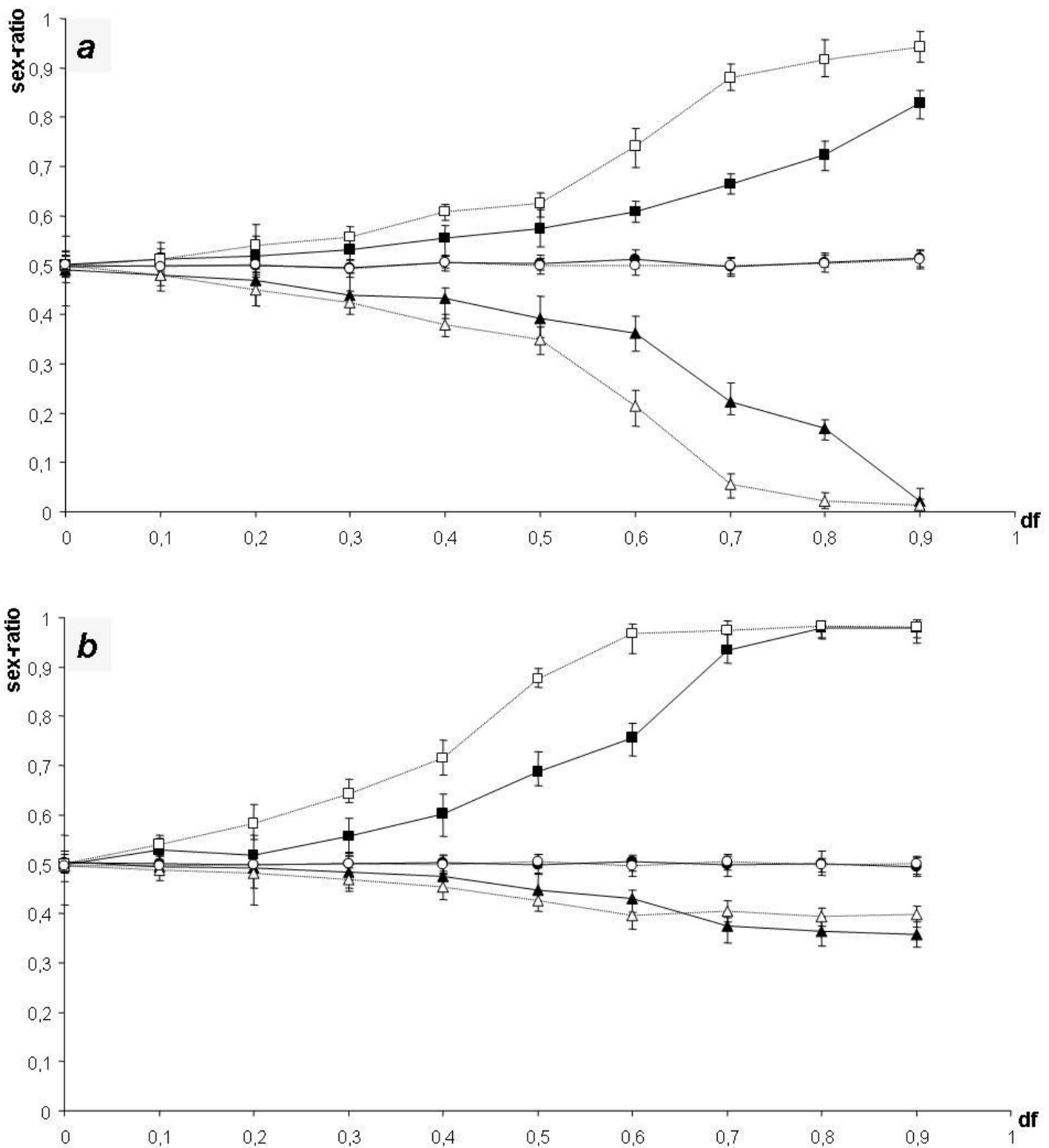


Figure 2
ESS sex ratios in GOOD habitats (G), POOR habitats (P) and in the whole population (SR_{tot}) as a function of female dispersal rate (d_f) in the model with habitat density-dependent regulation. (a): $g = 0.3$. (b): $g = 0.7$. Bars show maximal and minimal values in 20,000 generations at the equilibrium. Triangles: G , squares: P and circles: SR_{tot} . Plain symbols: $F = 1.5$, open symbols: $F = 2$. Results are shown for simulations run with initial allele values of G_1, G_2, P_1 and $P_2 = 0.5$.

habitat may become totally biased ($P = 1$ or $G = 0$). This is illustrated in fig. 2b by $g = 0.7$, $F = 2$ and $d_f = 0.9$.

TOTAL density-dependent regulation (fig. 3)

For $d_f = 0$ (total philopatry), females nest only in GOOD habitats and the situation is the same as with a single population nesting in a homogeneous environment ($G = SR_{tot} = 0.5$). For $0 < d_f < 1$ (partial philopatry), the sex ratio is always biased towards males in POOR habitats and towards females in GOOD habitats ($G < 0.5 < P$) like in the HABITAT model. For low values of d_f , only males are produced in POOR habitats ($P = 1$) and the sex ratio in GOOD habitats is such that $SR_{tot} = 0.5$. In contrast with the HABITAT model (i) as soon as $d_f > 0$, the sex ratio is here totally male biased in POOR habitats, even for low values of F , and (ii) as long as $F > 1$, a decrease of F leads the sex ratio in GOOD habitats to be more female biased. When d_f increases, the sex ratio in GOOD habitats is more and more female biased until it may become totally biased ($G = 0$) as well. When $G = 0$, a further increase of d_f leads the sex ratio in POOR habitats to decrease ($P < 1$) and SR_{tot} to increase ($SR_{tot} > 0.5$). This is illustrated in fig. 3a by $g = 0.3$, $F = 1.4$ and $d_f = 0.9$.

Discussion

Interpretation of the results and comparison with previous models

From our simulation results, we identify 2 evolutionary forces leading to the ESS sex ratios in our models. The first force is the consequence of mating taking place in a unique area for the entire population, leading SR_{tot} to be equal to 0.5 [22]. The second force (habitat selection) is due to the difference in quality between habitats and the difference in dispersal rate between sexes: because females are always the less dispersing sex unless $d_f = 1$, female offspring should be under-produced in POOR habitat and overproduced in GOOD habitats in order to increase the likelihood that females will nest in GOOD habitat [16].

In the HABITAT model, in case of high female philopatry (low d_f values), the overproduction of female offspring in GOOD habitats may lead to a high number of females returning in GOOD habitats to nest, and thus to a higher competition for resources in GOOD habitats compared to POOR habitats. In the case of low female philopatry (high d_f values), nesting females are more evenly distributed between habitats, and the strength of the competition for resources in GOOD habitats decreases. For a given value of d_f , the optimal distribution of adults between habitats (i.e. when the competition for resources is equal between habitats) is attained when there are F times more females nesting in GOOD habitats than females nesting in POOR habitats (ideal free distribution of nests [36]). For $d_f = 0$, this is obtained with unbiased sex ratios ($G = P = 0.5$). For $d_f > 0$, the female bias in GOOD habitats increases with

higher values of d_f in order to reach the ideal free distribution of nests. When F increases, GOOD habitats can receive more females per unit of resource, and the sex ratio is then more biased towards females in GOOD habitats.

To sum up, a strategy of sex ratio must fulfil two conditions to be an ESS in the HABITAT model: (i) The sex ratio of the whole population is equilibrated; (ii) The number of nesting females per unit of resource is F times larger in GOOD habitats than in POOR habitats. These two conditions derived from our verbal argument can be expressed mathematically as:

$$(i) \quad SR_{tot} = 0.5 \Leftrightarrow \frac{Fg(1-G) + (1-g)(1-P)}{Fg + (1-g)} = 0.5$$

$$(ii) \quad \frac{N_g}{Fg} = \frac{N_p}{1-g} \Leftrightarrow \frac{1-P}{1-G} = \frac{F(Fgd_f - 1 + d_f - gd_f)}{(1-g)d_f - F(1-gd_f)}$$

with N_p and N_g the number of female nesting in POOR and GOOD habitats, respectively. When the second condition leads the sex ratio in POOR habitats to be totally male biased ($P = 1$), the sex ratio in GOOD habitats is determined by the first condition ($SR_{tot} = 0.5$). This case is illustrated in fig. 2b for $g = 0.7$, $F = 2$ and $d_f = 0.8$. When the second condition leads the sex ratio in GOOD habitats to be totally female biased ($G = 0$), the Fisherian force still favours an unbiased sex ratio for the entire population ($SR_{tot} = 0.5$) while the habitat selection force favours the production of more males in POOR habitats. The two selective forces then equilibrate for $G = 0$ and for an intermediate value of P , with $P > 0.5$ and $SR_{tot} > 0.5$. The sex ratio of the whole population is male-biased but stays close to 0.5 (results not shown).

In the TOTAL model, the first force, conducting SR_{tot} to be unbiased, is the same as in the HABITAT model. However, the habitat selection force is different: because there is no density-dependent regulation in habitats, a nest in a POOR habitat always produces F times fewer adults in the next generation than a nest in a GOOD habitat. So, it is always more advantageous for females to nest in GOOD habitats. Whatever the values of d_f and g , the probability to nest in GOOD habitats is higher for females born in GOOD habitats than for females born in POOR habitats. Consequently, females should be produced in GOOD habitats rather than in POOR habitats. For males, regardless of the habitat where they are born, the probability of mating with a female that will nest in a GOOD habitat is the same. Hence, the second force selects against the production of females in POOR habitats, resulting in the production of males only. In GOOD habitats, the ESS sex ratio is the one that permits SR_{tot} to be equilibrated. These

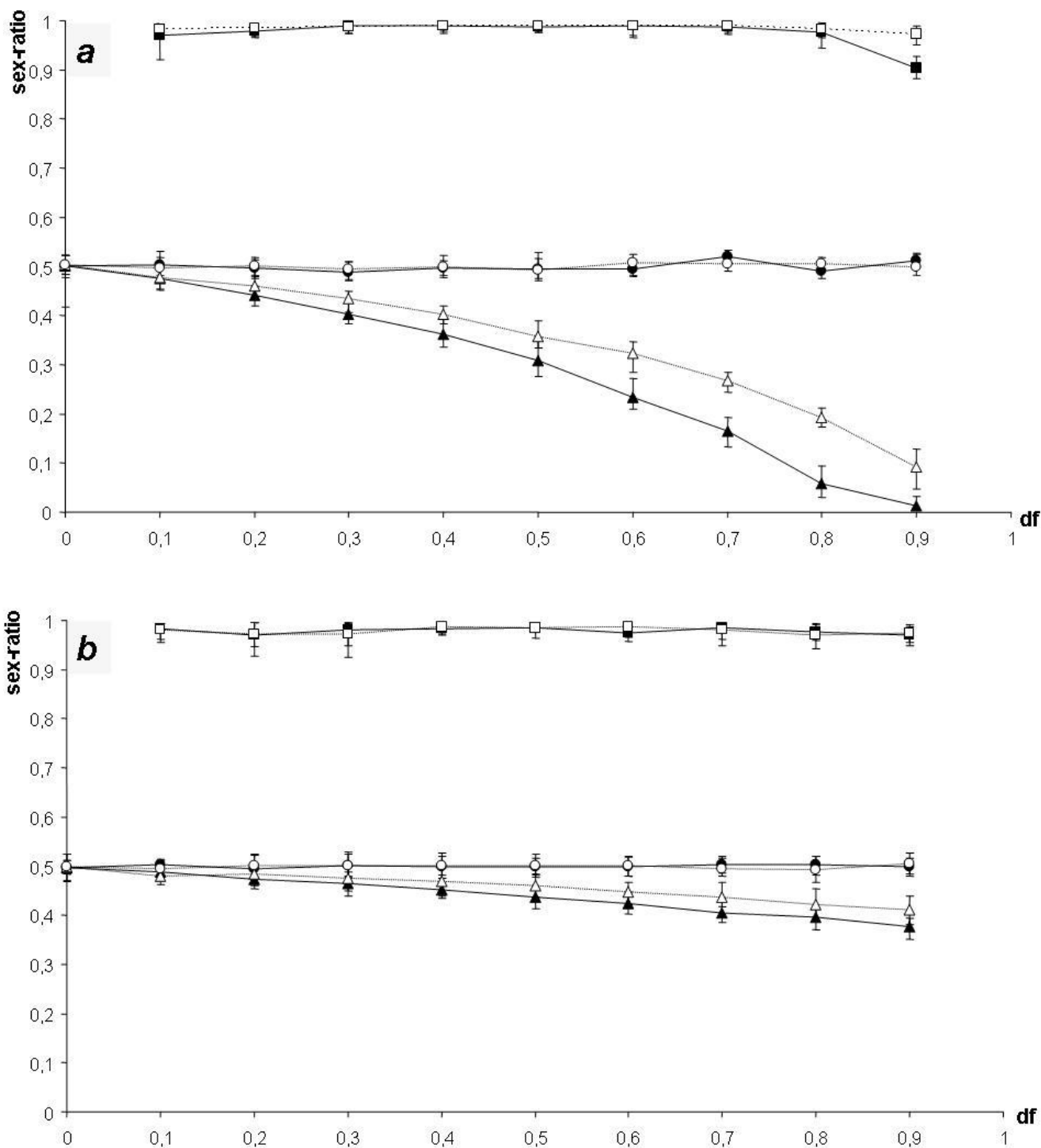


Figure 3
ESS sex ratios in GOOD habitats (G), POOR habitats (P) and in the whole population (SR_{tot}) as a function of female dispersal rate (d_f) in the model with total density-dependent regulation. (a): $g = 0.3$. (b): $g = 0.7$. Bars show maximal and minimal values in 20,000 generations at the equilibrium. Triangles: G, squares: P, and circles: SR_{tot} . Plain symbols: $F = 1.4$, open symbols: $F = 2$. Results are shown for simulations run with initial allele values of G_1, G_2, P_1 and $P_2 = 0.5$.

two conditions derived from our verbal argument can be expressed mathematically as:

$$(i) \quad P = 1$$

$$(ii) \quad SR_{tot} = 0.5 \Leftrightarrow \frac{FN_g(1-G)}{FN_g + N_p} = 0.5 \Leftrightarrow G = 0.5 \left(1 - \frac{d_f(1-g)}{F(1-d_f + gd_f)} \right)$$

with N_p and N_g the numbers of females nesting in POOR and GOOD habitats, respectively. When F increases, GOOD habitats produce more individuals compared to POOR habitats, so the ESS sex ratio in GOOD habitats needs to be less female biased to equilibrate the global sex ratio.

When it is not possible to satisfy these two conditions simultaneously (i.e. when $F < d_f(1-g)/(1-d_f+gd_f)$), the habitat selection force still favours a totally male-biased sex ratio in POOR habitats, while the Fisherian force favours the production of some females in POOR habitats so that $SR_{tot} = 0.5$. The two selective forces then equilibrate for $G = 0$ and for an intermediate value of P , with $P < 1$ and $SR_{tot} > 0.5$. The sex ratio of the whole population is male-biased but stays close to 0.5. This case is illustrated in fig. 3b for $g = 0.3$, $F = 2$ and $d_f = 0.9$.

With either kind of density-dependent regulation, our results show that partial female philopatry ($0 < d_f < 1$) leads the ESS sex ratio to be biased towards males in POOR habitats and towards females in GOOD habitats. Extremely biased sex ratios are obtained for higher values of F and d_f in our HABITAT model and most values of d_f and F in our TOTAL model. We predict extraordinary sex ratios for ordinary values of parameters, especially in the TOTAL model where only males may be produced in POOR habitats. These conditions are likely to be met in many situations involving female philopatry, including the case of sea turtles (see below). The population size assumed in our model is quite large and the population is panmictic. Therefore, the selective forces resulting from kin competition (Local Mate Competition and Local Resource Competition [13,37]) have no influence.

The density-dependent regulation in our HABITAT model is the same as in Julliard [16]. However, here both sexes migrate before mating in an area distinct from nesting habitats. The results of Julliard's model and ours are similar on 2 points: (i) ESS sex ratios are male-biased in POOR habitats and female-biased in GOOD habitats, and (ii) the bias of ESS sex ratio increases when the female philopatry decreases. In contrast with Julliard, we find an unbiased ESS sex ratio for the overall population. Guillon *et al.* [38] have refined the model of Julliard [16] by calculating reproductive values in a more comprehensive way. Total male dispersal ($d_m = 1$) in their model yields the

same results as our HABITAT model, although the life cycles modelled are indeed different.

A promising model by Reinhold [25] has already proposed that female philopatry and spatial heterogeneity offer the conditions for the evolution of environmental sex determination in reptiles. This study assumed the same global density-dependent regulation as in our TOTAL model and concluded that a sex ratio strategy biased towards males in low-quality sites and towards females in high-quality sites was favoured relatively to unbiased sex ratios resulting from genetic sex determination. The method used by Reinhold did not allow him to find the values for the ESS sex ratios, yet his results suggested that the sex ratio was equilibrated at the whole population scale. Reinhold [25] also restricted the range of his parameters: (i) high-quality habitats were assumed to be rare (equivalent in our model to $g < 0.5$), and (ii) the proportion of females born in low-quality sites but nesting in high-quality sites was constrained by the difference in habitat quality (equivalent to $Fd_f(1-g) < F - 1$ in our model, i.e. high female philopatry or high difference in habitat quality). We here show that biased sex ratios strategies can invade and get to fixation beyond Reinhold's range of parameters. Indeed, low F and high d_f values are biologically realistic and give the most extreme sex ratios in our study, these results being quite unexpected. Furthermore, we obtain the values for the ESS sex ratio and show why equilibrated population sex ratio is a necessary condition for ESS in most cases. In contrast, Freedberg and Wade [31] have proposed that inheritance of nest-site through female philopatry could lead to female biased sex-ratio at the level of the whole population. Their conclusion was not based on an ESS analysis and is therefore difficult to compare to our results.

Implications for the evolution of TSD in reptiles

The model may apply to any species with Environmental Sex Determination or with maternal control of sex allocation that fits our main assumptions, namely heterogeneity of habitat quality and female philopatry. The case of sea turtles, which is probably the most documented one, is discussed below.

The first key assumption of the model is that the environment is heterogeneous with respect to survival from oviposition to reproduction. The model then predicts that the primary sex ratio should adjust to the quality of the nesting environment, with more females being produced at high quality habitats and more males at low quality habitats. For species where females are produced at high incubation temperature (TSD Ia), this would be the case if temperature during incubation positively correlates with nest success. Heterogeneity in temperature has often been described between neighbouring nesting beaches, due to

difference in composition or albedo of the sand [e.g., [32,39]]. Temperature heterogeneity can also be found within a nesting beach. The cooling effect of tides creates a decrease of temperature from higher to lower beach zone [34,40-42], and the back of the beach may be cooler than the open beach, due to the presence of shadowing vegetation [43,44]. Interestingly, low temperature beaches or zones are often associated with a relatively lower hatching success [[32,34,39,41,42,45], but see [46]]. Indeed, nests on the lower beach can be lost due to erosion or inundation [33,34,47-52], and nests in the vegetation zone may suffer a higher predation rate or rupture risk [53-55]. In addition, nests in the lower beach zone may be more at risk of inundation by rainfall [56,57] and hatchlings emerging in the vegetation zone may face orientation problems in finding the sea [49,58,59]. Low temperature itself could influence hatching success by slowing the development of embryos and thus increase incubation time and thereby the risk of loss, destruction or predation. Overall, on many nesting grounds, even though excessively high temperatures can have detrimental effects on incubation process [60], a higher nest success could correlate with relatively high, feminizing, temperatures, as predicted by the model.

The present model investigates the consequences of female philopatry on the ESS sex ratio. Adult natal philopatry is difficult to observe in species with delayed sexual maturity, such as sea turtles because of the long time between birth and the first reproduction event. Nevertheless, the use of maternally inherited genetic markers (mitochondrial DNA) has provided support for female natal homing at a regional scale [e.g., [61-64]]. At a finer spatial scale, genetic isolation by distance of female green turtles has been observed on the beach of Tortuguero [65]. In addition, nest site fixity, i.e. the tendency for an individual female to cluster its nests, has been observed within a given season (re-nesting events) at the scale of different beaches [e.g., [48,49,66-68]], along the coastal axis of a nesting beach [e.g., [26,44,69]] or along the vegetation to ocean axis [44,59]. The same behaviour has also been observed for female sea turtles nesting in several breeding seasons (remigration events) [26,28,48,67,70]. Overall, although female sea turtles seem to be highly philopatric to their natal region, further work is still needed to test the model's predictions. In this aim, studies of female philopatry in relation with spatial variation of nesting success and sex ratios would be greatly valuable.

Destruction of previous nests by nesting females has been observed on several beaches [71,72]. Caut *et al.* [73] have shown that such a covering of nests may also be detrimental to the incubation success of the overlaying nest. At saturation, the incubation success of the nesting area is expected to tend to a finite rate, depending on the carrying

capacity of the laying environment. This is the basis for the density-dependent regulation assumed in our HABI-TAT model. Such a saturation may be rarely observed now, given the important human pressure on sea turtle populations in the recent years by egg poaching, turtle hunting and accidental catching [74], but could have been reached in the past when sea turtles were much more abundant. Alternatively, populations could be regulated at the sea, by predation on juveniles or by competition for food, as described in our TOTAL model. If density-dependent regulation occurs at both levels (first on nesting beaches and then at sea), the evolution of sex ratio should follow the same pattern as in the case of HABITAT density-dependent regulation alone. Indeed, this would modify the HABITAT model only by adding a random draw of individuals from the adult population.

The model's assumptions may be satisfied in other species of turtles. In freshwater turtles, nest temperature could be positively correlated with hatching success [[75-77], but see [78]]. Female freshwater turtles exhibit nest site-fidelity [e.g., [79-82]]. Furthermore, molecular studies have found significant genetic structure among nearby nesting sites [83,84] or genetic isolation by distance within a nesting site [82], suggesting that natal homing is present in freshwater turtles too.

Perspectives for refining the model

An important feature of the model is panmixia, resulting from the absence of male philopatry. This assumption may be violated in a variety of species. Further modelling is warranted to investigate the consequences of relaxing the hypothesis of panmixia, but preliminary work indicates that the predicted sex ratios are very similar as long as females are more philopatric than males.

In the present model, generations are discrete; i. e. individuals reproduce only once before dying. Describing a long-lived species, with a juvenile phase and multiple reproductive episodes, is not expected to change the predictions of the model. Only the time needed to reach the ESS should increase [85]. However, introducing a temporally variable environment is expected to change the predictions of the model, especially in the case of overlapping generations. The intensity of the habitat selection force should decrease as the habitat becomes less predictable from one generation to the next. Further work would be useful to study the influence of temporal variation of habitat quality on the ESS sex ratios.

Another improvement of the model could be to allow females to prefer high quality sites. In the HABITAT model, perfect habitat selection by dispersing females (a GOOD habitat is chosen F times more often than a POOR habitat), leads to an ideal free distribution of breeding

females. This should cancel the advantage of sex ratio biasing [16,38]. In contrast, unless $d_f = 1$, perfect habitat selection in the TOTAL model would not equalize the probabilities of different females reaching a GOOD habitat, and is thus not expected to yield equilibrate ESS sex ratios.

In our model, female dispersal can be considered as an imperfect philopatry resulting from constraints on orientation, migration or perception of the environment. Alternatively, dispersal could result from selection in a temporally variable environment: when the quality of the habitat is not completely predictable, individuals should adopt a strategy that permits them to explore other breeding-sites. It would thus be interesting to allow the joint evolution of sex allocation and dispersal rate [86].

Conclusion

Our individual-based simulation model shows that female nest-site philopatry and heterogeneity of habitat quality provide sufficient conditions for the evolution of biased habitat-dependent sex ratios. In all cases, the evolutionary stable strategy is to overproduce females in good quality habitats and males in low quality habitats, while the sex ratio of the overall population is generally unbiased. The values for the ESS sex ratios are strongly dependent on the type of density-dependent regulation assumed. Highly biased sex ratios are predicted for biologically realistic values of parameters corresponding to low female philopatry and moderate difference in habitat quality.

To assess the contribution of our model in the study of the evolutionary significance of temperature-dependent sex determination, it should be tested in sea turtles by measuring sex ratios and incubation success of natural nests. We predict a positive correlation between incubation success, measured as the proportion of eggs yielding juveniles that reach the sea, and the proportion of females among hatchlings. In sea turtles, high temperatures during incubation lead to the overproduction of females in hatchlings. Preliminary evidence suggests that higher incubation success could be correlated with high (feminizing) temperatures. However, field studies are needed to obtain more convincing evidence.

Methods

We search for the ESS values of sex ratio for different values of F , g and d_f . At each generation i , we compute G^i as the mean of alleles at the G locus in the adult population and P^i as the mean of alleles at the P locus in the adult population. The total population sex ratio, SR_{tot}^i , is calculated as the number of males divided by 5,000 (the total number of adults). The simulations are run until values of

G^i , P^i and SR_{tot}^i are stable. We then compute G , P and SR_{tot} means of G^i , P^i and SR_{tot}^i , respectively, during 20,000 generations at the equilibrium. We take into account variations between generations by recording the maximum and minimum of G^i , P^i and SR_{tot}^i during this period. For defined values of F , g and $d_f < 1$, similar values are found for G , P and SR_{tot} regardless of the initial values of G_1 , G_2 , P_1 and P_2 . In the absence of philopatry ($d_f = 1$), depending on the simulation, we obtain different equilibrium values for sex allocations in GOOD and POOR habitats (G , P) such that $SR_{tot} = 0.5$. Hence, results for $d_f = 1$ are not presented in the figures.

Authors' contributions

VH wrote the program, carried out the simulations and drafted the manuscript.

JMG participated in the design of the study and drafted the manuscript.

All authors read and approved the final manuscript.

Acknowledgements

We thank Marc Girondot, Richard Hall, Romain Julliard, Lucie Salvaudon and Jacqui Shykoff and two anonymous reviewers for helpful comments on previous versions of the manuscript, Marion Flamant for her assistance.

References

1. Waser PM, Jones WT: **Natal philopatry among solitary mammals.** *The Quarterly Review of Biology* 1983, **58**:355-390.
2. Welty JC, Baptista L: **The life of birds.** New York, Saunders College Publishing; 1988.
3. Meylan A, Bowen BW, Avise JC: **A genetic test of the natal homing versus social facilitation models for green turtle migration.** *Science* 1990, **248**:724-727.
4. Gold JR, Richardson LR, Turner TF: **Temporal stability and spatial divergence of mitochondrial DNA haplotype frequencies in red drum (*Sciaenops ocellatus*) from coastal regions of the western Atlantic Ocean and Gulf of Mexico.** *Marine Biology* 1999, **133**:593-602.
5. Clarke AL, Saether BE, Roskaft E: **Sex biases in avian dispersal: a reappraisal.** *Oikos* 1997, **79**:429-438.
6. Pardini AT, Jones CS, Noble LR, Kreiser B, Malcolm H, Bruce BD, Stevens JD, Cliff G, Scholl MC, Francis M, Duffy CAJ, Martin AP: **Sex-biased dispersal of great white sharks.** *Nature* 2001, **412**:139-140.
7. Greenwood P: **Mating systems, philopatry and dispersal in birds and mammals.** *Animal Behaviour* 1980, **28**:1140-1162.
8. Liberg O, Von Schantz T: **Sex-biased philopatry and dispersal in birds and mammals: the Oedipus hypothesis.** *American Naturalist* 1985, **126**:129-135.
9. Wolff JO, Plissner JH: **Sex biases in avian natal dispersal: an extension of the mammalian model.** *Oikos* 1998, **83**:327-330.
10. Lindberg MS, Sedinger JS, Derksen DV, Rockwell RF: **Natal and Breeding Philopatry in a Black Brant, *Branta bernicla nigricans*, Metapopulation.** *Ecology* 1998, **79**:1893-1904.
11. Schjorring S: **Ecologically determined natal philopatry within a colony of great cormorants.** *Behavioral Ecology* 2002, **12**:287-294.
12. Kawecki TJ: **Sex-biased dispersal and adaptation to marginal habitats.** *American Naturalist* 2003, **162**:415-426.

13. Hamilton WD: **Extraordinary sex ratios.** *Science* 1967, **156**:477-488.
14. Cockburn A, Legge S, Double MC: **Sex ratios in birds and mammals: can the hypotheses be disentangled?** In *Sex Ratios: Concepts and Research Methods* Edited by: Hardy ICW. , Cambridge; 2003:266-286.
15. Komdeur J, Daan S, Tinbergen J, Mateman C: **Extreme adaptive modification in sex ratio of the Seychelles warblers eggs.** *Nature* 1997, **385**:522-525.
16. Julliard R: **Sex-specific dispersal in spatially varying environments leads to habitat-dependent evolutionarily stable offspring sex ratios.** *Behavioral Ecology* 2000, **11**:421-428.
17. Bull JJ, Charnov EL: **Enigmatic reptilian sex ratios.** *Evolution* 1989, **43**:1561-1566.
18. Ewert MA, Nelson CE: **Sex determination in turtles: diverse patterns and some possible adaptive values.** *Copeia* 1991, **1**:50-69.
19. Burke RL: **Adaptive value of sex determination mode and hatchling sex ratios bias in reptiles.** *Copeia* 1993, **3**:854-859.
20. Shine R: **Why is sex determined by nest temperature in many reptiles?** *Trends in Ecology and Evolution* 1999, **14**:186-189.
21. Shine R: **Reply from Richard Shine.** *Trends in Ecology and Evolution* 1999, **14**:360.
22. Fisher RA: **The Genetical Theory of Natural Selection.** Oxford, Clarendon Press; 1930.
23. Charnov EL, Bull JJ: **When is sex environmentally determined?** *Nature* 1977, **266**:828-830.
24. Warner DA, Shine R: **The adaptive significance of temperature-dependent determination: experimental tests with a short-lived lizard.** *Evolution* 2005, **59**:2209-2221.
25. Reinhold K: **Nest-site philopatry and selection for environmental sex determination.** *Evolutionary Ecology* 1998, **12**:245-250.
26. Carr A, Carr MH: **Site fixity in the caribbean green turtle.** *Ecology* 1972, **53**:425-429.
27. Bowen BW: **Molecular genetic studies of marine turtles.** In *Biology and conservation of sea turtles* Edited by: Bjornedal KA. Washington D.C., Smithsonian Institute Press; 1995.
28. Gyuris E, Limpus CJ: **The loggerhead turtle *Caretta caretta* in Queensland: population breeding structure.** *Australian Wildlife Research* 1988, **15**:197-209.
29. FitzSimmons NN, Moritz C, Limpus CJ, Pope L, Prince R: **Geographic structure of mitochondrial and nuclear gene polymorphisms in Australian green turtle populations and male-biased gene flow.** *Genetics* 1997, **147**:1843-1854.
30. Roberts MA, Schwartz TS, Karl SA: **Global population genetic structure and male-mediated gene flow in the green sea turtle (*Chelonia mydas*): analysis of microsatellite loci.** *Genetics* 2004, **166**:1857-1870.
31. Freedberg S, Wade MJ: **Cultural inheritance as a mechanism for population sex-ratio bias in reptiles.** *Evolution* 2001, **55**:1049-1055.
32. Limpus CJ, Reed PC, Miller JD: **Island and turtles: the influence of choice of nesting beach on sex ratio; ; Townsville.** Edited by: Baker JT, Carter RM and Sammarco PW. JCU Press; 1983:397-402.
33. Mrosovsky N: **Ecology and nest-site selection of leatherback turtles *Dermochelys coriacea*.** *Biological Conservation* 1983, **26**:47-56.
34. Hays GC, Speakman JR: **Nest placement by loggerhead turtles, *Caretta caretta*.** *Animal Behaviour* 1993, **45**:47-53.
35. De Meeüs T: **Adaptive diversity, specialisation, habitat preference and parasites.** In *Evolutionary biology of host-parasite relationships: theory meets reality* Edited by: Poulin R, Morand S and Skorping A. Amsterdam, Elsevier Science; 2000:27-42.
36. Fretwell SD, Lucas HLJ: **On territorial behaviour and other factors influencing habitat distribution in birds.** *Acta Biotheoretica* 1970, **19**:16-36.
37. Courteau J, Lessard S: **Optimal sex ratios in structured populations.** *Journal of Theoretical Biology* 2000, **207**:159-175.
38. Guillon JM, Julliard R, Leturque H: **Evolution of habitat-dependent sex allocation in plants: superficially similar to, but intrinsically different from animals.** *Journal of Evolutionary Biology* 2006, **19**:500-512.
39. Hays GC, Adams CR, Mortimer JA, Speakman JR: **Inter- and intra-beach thermal variation for green turtle nests on Ascension Island, South Atlantic.** *Journal of the Marine Biological Association of United Kingdom* 1995, **75**:405-411.
40. Mrosovsky N, Dutton PH, Whitmore CP: **Sex-ratios of 2 species of sea turtle nesting in Suriname.** *Canadian Journal of Zoology* 1984, **62**:2227-2239.
41. Leslie AJ, Penick DN, Spotila JR, Paladino FV: **Leatherback turtle, *Dermochelys coriacea*, nesting and nest success at Tortuguero, Costa Rica, in 1990-1991.** *Chelonian Conservation and Biology* 1996, **2**:159-168.
42. Lopez-Castro MC, Carmona R, Nichols WJ: **Nesting characteristics of the olive ridley turtle (*Lepidochelys olivacea*) in Cabo Pulmo, southern Baja California.** *Marine Biology* 2004, **145**:811-820.
43. Mrosovsky N, Hopkins-Murphy SR, Richardson JE: **Sex ratios of sea turtles: seasonal changes.** *Science* 1984, **225**:739-741.
44. Kamel SJ, Mrosovsky N: **Repeatability of nesting preferences in the hawksbill sea turtle, *Eretmochelys imbricata*, and their fitness consequences.** *Animal Behaviour* 2005, **70**:819-828.
45. Horrocks JA, Scott NMA: **Nest site location and nest success in the hawksbill turtle *Eretmochelys imbricata* in Barbados, West Indies.** *Marine Ecology Progress Series* 1991, **69**:1-8.
46. Hewavisenthi S, Parmenter CJ: **Incubation environment and nest success of the flatback turtle (*Natator depressus*) from a natural nesting beach.** *Copeia* 2002, **2**:302-312.
47. Bacon PR: **Studies on the leatherback turtle (*Dermochelys coriacea*) in Trinidad, West Indies.** *Biological Conservation* 1970, **2**:213-217.
48. Schulz JP: **Sea turtles nesting in Surinam.** *Zoologische Verhandlungen Rijksmuseum van Natuurlijke Historie Leiden* 1975, **143**:1-143.
49. Diamond AW: **Breeding biology and conservation of hawksbill turtles, *Eretmochelys imbricata* L., on Cousin Island, Seychelles.** *Biological Conservation* 1976, **9**:199-215.
50. Mortimer JA: **Factors influencing beach selection by nesting sea turtles.** In *Biology and Conservation of sea turtles* Edited by: Bjornedal KA. Washington D. C., Smithsonian Institution Press; 1982.
51. Boulon RH, McDonald DL, Dutton DL: **Leatherback turtles (*Dermochelys coriacea*) on St. Croix, U.S. Virgin Islands: Fifteen years of Conservation.** *Chelonian Conservation and Biology* 1996, **2**:141-147.
52. Oz M, Erdogan A, Kaska Y, Dusen S, Aslan A, Sert H, Yavuz M, Tunc MR: **Nest temperatures and sex-ratio estimates of loggerhead turtles at Patara beach on the southwestern coast of Turkey.** *Canadian Journal of Zoology* 2004, **82**:94-101 [<http://article.pubs.nrc-cnrc.gc.ca/ppv/RPViewDoc?handler=HandleInitialGet&journal=cjz&volume=82&calyLang=eng&articleFile=z03-200.pdf>].
53. Fowler LE: **Hatching success and nest predation in the green sea turtle, *Chelonia mydas*, at Tortuguero, Costa Rica.** *Ecology* 1979, **60**:946-955.
54. Whitmore CP, Dutton PH: **Infertility, embryonic mortality and nest-site selection in leatherback and green sea turtles in Suriname.** *Biological Conservation* 1985, **34**:251-272.
55. Maros A, Louveaux A, Godfrey MH, Girondot M: **Scapteriscus didactylus (Orthoptera, Gryllotalpidae), predator of leatherback turtle eggs in French Guiana.** *Marine Ecology Progress Series* 2003, **249**:289-296.
56. Ragotzkie RA: **Mortality of loggerhead turtle eggs from excessive rainfall.** *Ecology* 1959, **40**:303-305.
57. Kraemer JE, Bell R: **Rain-induced mortality of eggs and hatchlings of loggerhead sea turtles (*Caretta caretta*) on the Georgia coast.** *Herpetologica* 1980, **36**:72-77.
58. Godfrey MH, Barreto R: **Beach vegetation and seafinding orientation of turtle hatchlings.** *Biological Conservation* 1995, **74**:29-32.
59. Kamel SJ, Mrosovsky N: **Nest site selection in leatherbacks, *Dermochelys coriacea*, individual patterns and their consequences.** *Animal Behaviour* 2004, **68**:357-366.
60. Matsuzawa Y, Sato K, Sakamoto W, Bjornedal KA: **Seasonal fluctuations in sand temperature: effects on the incubation and mortality of loggerhead sea turtle (*Caretta caretta*) pre-emergent hatchlings in Minabe, Japan.** *Marine Biology* 2002, **140**:639-646.
61. Norman JA, Moritz C, Limpus CJ: **Mitochondrial DNA control region polymorphisms (genetic markers for ecological studies of marine turtles).** *Molecular Ecology* 1994, **3**:363-373.
62. Laurent L, Casale P, Bradai MN, Godley BJ, Gerosa G, Broderick AC, Schroth W, Schierwater B, Levy AM, Freggi D, Abd El-Mawla EM,

- Hadoud DA, Gomati HE, Domingo M, Hadjichristophorou M, Kornarak L, Demirayak F, Gautier C: **Molecular resolution of marine turtle stock composition in fishery bycatch: a case study in the Mediterranean.** *Molecular Ecology* 1998, **7**:1529-1542.
63. Bass A: **Genetic analysis to elucidate the natural history and behaviour of hawksbill turtles (*Eretmochelys imbricata*) in the wider Caribbean: a review and re-analysis.** *Chelonian Conservation and Biology* 1999, **3**:195-199.
64. Lopez-Castro MC, Rocha-Olivares A: **The panmixia paradigm of eastern Pacific olive ridley turtles revised: consequences for their conservation and evolutionary biology.** *Molecular Ecology* 2005, **14**:3325-3334.
65. Pearce T, Parker PG: **Local genetic structure within two rookeries of *Chelonia mydas* (the green turtle).** *Heredity* 1996, **77**:619-628.
66. Williams-Walls N, O'Hara J, Gallagher RM, Worth DF, Peery BD, Wilcox JR: **Spatial and temporal trends of sea turtle nesting on Hutchinson Island, Florida, 1971-1979.** *Bulletin of Marine Science* 1983, **33**:55-66.
67. Mortimer JA, Portier KM: **Reproductive homing and internesting behaviour of the green turtle (*Chelonia mydas*) at Ascension Island, South Atlantic Ocean.** *Copeia* 1989, **4**:962-977.
68. Steyermark AC, Williams K, Spotila JR, Paladino FV, Rostal DC, Morreale SJ, Koberg MT, Arauz R: **Nesting leatherback turtles at Las Baulas de Guanacaste National Park, Costa Rica.** *Chelonian Conservation and Biology* 1996, **2**:173-183.
69. Talbert OR Jr., Stancyk SE, Dean JM, Will JM: **Nesting activity of the loggerhead turtle (*Caretta caretta*) in South Carolina. I: A rookery in transition.** *Copeia* 1980, **4**:709-719.
70. Bjorndal KA, Carr A, Meylan A, Mortimer JA: **Reproductive-biology of the hawksbill *Eretmochelys imbricata* at Tortuguero, Costa Rica, with notes on the ecology of the species in the Caribbean.** *Biological Conservation* 1985, **34**:353-368.
71. Bustard HR, Tognetti KP: **Green sea turtles: a discrete simulation of density-dependent population regulation.** *Science* 1969, **163**:939-941.
72. Girondot M, Tucker AD, Rivalan P, Godfrey MH, Chevalier J: **Density-dependent nest destruction and population fluctuations of Guianan leatherback turtles.** *Animal Conservation* 2002, **5**:75-84.
73. Caut S, Hulin V, Girondot M: **Impact of density-dependent nest destruction on emergence success of Guianan leatherback turtles (*Dermochelys coriacea*).** *Animal Conservation* 2006, **9**:189-197.
74. Pritchard PCH: **The conservation of sea turtles: practices and problems.** *American Zoologist* 1980, **20**:609-617.
75. Cagle KD, Packard GC, Miller K, Packard MJ: **Effects of the microclimate in natural nests on development of embryonic painted turtles, *Chrysemys picta*.** *Functional Ecology* 1993, **7**:653-660.
76. Valenzuela N: **Constant, shift, and natural temperature effects on sex determination in *Podocnemis expansa* turtles.** *Ecology* 2001, **82**:3010-3024.
77. Kolbe JJ, Janzen FJ: **Impact of nest-site selection on nest success and nest temperature in natural and disturbed habitats.** *Ecology* 2002, **83**:269-281.
78. Ewert MA, Jackson DR, Nelson CE: **Patterns of temperature-dependent sex determination in turtles.** *Journal of Experimental Zoology* 1994, **270**:3-15.
79. Standing KL, Herman TB, Morrison IP: **Nesting ecology of Blanding's turtle (*Emydoidea blandingii*) in Nova Scotia, the north-eastern limit of the species' range.** *Canadian Journal of Zoology* 1999, **77**:1609-1614.
80. Janzen FJ, Morjan CL: **Repeatability of microenvironment-specific nesting behaviour in a turtle with environmental sex determination.** *Animal Behaviour* 2001, **62**:73-82.
81. Tucker AD: **Nesting red-eared sliders (*Trachemys scripta elegans*) exhibit fidelity to their nesting areas.** *Journal of Herpetology* 2001, **35**:661-664.
82. Freedberg S, Ewert MA, Ridenhour BJ, Neiman M, Nelson CE: **Nesting fidelity and molecular evidence for natal homing in the freshwater turtle, *Graptemys kohnii*.** *Proceedings of the Royal Society of London* 2005, **272**:1345-1350.
83. Scribner KT, Congdon JD, Chesser RK, Smith MH: **Annual differences in female reproductive success affect spatial and cohort-specific genotypic heterogeneity in painted turtles.** *Evolution* 1993, **47**:1360-1373.
84. Valenzuela N, Janzen FJ: **Nest-site philopatry and the evolution of temperature-dependent sex determination.** *Evolutionary Ecology Research* 2001, **3**:779-794.
85. Charlesworth B: **Evolution in age-structured populations.** In *Cambridge Studies in Mathematical Biology Volume 1*. Edited by: Cannings C and Hoppensteadt F. Cambridge, Cambridge University Press; 1980:300.
86. Leturque H, Rousset F: **Joint evolution of sex ratio and dispersal: conditions for higher dispersal rates from good habitats.** *Evolutionary Ecology* 2003, **17**:67-84.

Publish with **BioMed Central** and every scientist can read your work free of charge

"BioMed Central will be the most significant development for disseminating the results of biomedical research in our lifetime."

Sir Paul Nurse, Cancer Research UK

Your research papers will be:

- available free of charge to the entire biomedical community
- peer reviewed and published immediately upon acceptance
- cited in PubMed and archived on PubMed Central
- yours — you keep the copyright

Submit your manuscript here:
http://www.biomedcentral.com/info/publishing_adv.asp

