

Oceanic residents, neritic migrants: a possible mechanism underlying foraging dichotomy in adult female loggerhead turtles (*Caretta caretta*)

Hideo Hatase · Kazuyoshi Omuta · Katsumi Tsukamoto

Received: 4 December 2009 / Accepted: 15 February 2010 / Published online: 9 March 2010
© Springer-Verlag 2010

Abstract To reveal the mechanism underlying intrapopulation variation in the use of feeding habitats (oceanic vs. neritic) by adult female loggerhead turtles (*Caretta caretta*), we compared telomere length in the epidermis (a proxy for age) between oceanic- and neritic-foraging recruits (first-time nesters). Based on egg-yolk stable isotope ratios, recruits at Yakushima Island, Japan, were clearly divided into small oceanic planktivores and large neritic benthivores. There were no significant differences in telomere length between oceanic and neritic foragers, suggesting that they start reproduction at similar ages. Turtles that experienced faster growing conditions during their oceanic early lives may achieve sexual maturity there, while others may move from oceanic areas into neritic habitats, switching diets from nutrient-poor macroplankton to nutrient-rich benthic fauna in order to compensate for their earlier slow growth rate and continue their sexual development, reaching maturity in neritic waters.

Introduction

Although adult females of several sea turtle species (loggerhead, *Caretta caretta*, and green, *Chelonia mydas*, turtles) were previously thought to be obligate benthivores in neritic habitats (where water depths are <200 m) (Bolten 2003a), recent studies have revealed that some individuals forage on planktonic prey in oceanic habitats (where depths are >200 m) as the juveniles do (Hatase et al. 2002b, 2006, 2007; Hawkes et al. 2006; Seminoff et al. 2008; Reich et al. 2010). Among adult female loggerhead turtles within some populations, foraging dichotomy is linked to body size, with small females mainly using oceanic habitats, whereas large females are mainly using neritic habitats (Hatase et al. 2002b, 2007; Hawkes et al. 2006; Reich et al. 2010). Similar foraging dichotomy has been observed also among large juvenile loggerheads captured in coastal waters of the Northwest Atlantic but not size-based (McClellan and Read 2007; Mansfield et al. 2009). Adult female loggerheads show fidelity to their respective foraging habitats (Hatase et al. 2002b). The mechanisms that produce and maintain the intrapopulation variation in the choice of feeding habitats by adult females are still unknown. This phenomenon may be interpreted as facultative habitat shifts during sea turtle ontogeny. Mechanisms of facultative habitat shifts, dispersal polymorphism, partial migration, facultative diadromy, or facultative paedomorphosis have been studied among more tractable organisms such as insects (e.g. Harrison 1980), fishes (e.g. Jonsson and Jonsson 1993), amphibians (e.g. Denoël et al. 2005), and birds (e.g. Lundberg 1988; Berthold 1991). For example, some salmonids select habitats according to early growth conditions (e.g. Thorpe 1986; Olsson et al. 2006); faster growing juveniles reside in a river throughout their lives, whereas others migrate from the river to the ocean or a

Communicated by R. Lewison.

Electronic supplementary material The online version of this article (doi:10.1007/s00227-010-1413-9) contains supplementary material, which is available to authorized users.

H. Hatase (✉) · K. Tsukamoto
Ocean Research Institute, University of Tokyo,
1-15-1 Minamidai, Nakano, Tokyo 164-8639, Japan
e-mail: hatase@ori.u-tokyo.ac.jp

K. Omuta
Yakushima Sea Turtle Research Group, 489-8 Nagata,
Yakushima, Kagoshima 891-4201, Japan

lake. If sea turtles make similar decisions on habitat use, juveniles that fortuitously encounter abundant prey and grow faster in oceanic habitats during their early lives would stay there to become oceanic foraging adults, whereas juveniles with slow growth in oceanic habitats would move from oceanic to neritic habitats in search of better growth opportunities. If this hypothesis is true, oceanic foragers would reach sexual maturity and start reproduction earlier than neritic foragers (Hatase et al. 2004).

To test the aforementioned hypothesis, information on both foraging habitats and ages for recruits (first-time nesters) must be collected. Based on previous findings obtained by simultaneously using stable isotope analysis and satellite telemetry (Hatase et al. 2002b), we can distinguish between female turtles that are oceanic or neritic foragers by measuring stable carbon and nitrogen isotope ratios ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$) in the yolks of their eggs. In the previous study, during the post-nesting season, turtles with low $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ indicative of oceanic planktivores moved to oceanic areas, whereas turtles with high $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ indicative of neritic benthivores moved to neritic areas. In general, oceanic macroplankton have lower $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ than neritic benthic animals due to the differences in primary producers on which they are based and the trophic status that they occupy (Michener and Schell 1994). Although skeletochronology has traditionally been used to estimate sea turtle ages (e.g. Avens and Goshe 2007), this method is destructive and therefore cannot be applied to endangered live sea turtles. Alternatively, telomere length in the epidermis shortens with age in the loggerhead turtle and is likely to be an age estimator for live sea turtles (Hatase et al. 2008). Telomeres are oligonucleotide repeats (TTAGGG for vertebrates) found at the end of eukaryotic chromosomes, with their attrition occurring during mitosis (Monaghan and Hausmann 2006). Measurement of epidermal telomere length is the best available non-invasive method at this time for estimating relative ages of live sea turtles (Hatase et al. 2008). Sea turtles are iteroparous and may demonstrate fidelity by returning to the same nesting beaches from distant feeding grounds every few years (Miller 1997). Thus, long-term tagging censuses of individual nesting females, even on relatively low-density nesting beaches, enable us to categorize turtles as recruits or remigrants (experienced nesters) (Hatase et al. 2002a, b).

In the present study, we first measured $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ in egg-yolks from loggerhead turtle recruits to determine their pre-nesting foraging habitats (oceanic or neritic). Second, we compared epidermal telomere length between oceanic and neritic foragers to test whether oceanic foragers start reproduction earlier than neritic foragers. Based on the

results obtained in this study, we propose a mechanism that could cause intrapopulation variation in feeding habitat use by adult female loggerhead turtles. Elucidating the mechanisms behind individual decision-making about habitat use will contribute to our understanding of the evolution of alternative life histories within a population.

Materials and methods

Sample collection

Patrols looking for nesting turtles were conducted on foot every night (2100 to 0500 h) at the adjacent Inakahama (1.0 km length) and Maehama (0.9 km) beaches (30°24'N, 130°26'E), Nagata, Yakushima Island, Kagoshima Prefecture, Japan, by at least two persons per beach, from 13 May to 30 June in 2008. Almost all sea turtles landing or nesting on these two beaches have been monitored by the Yakushima Sea Turtle Research Group throughout the nesting season (April to August) annually since 1985 (Omuta 1997). Female loggerheads were identified by placing external plastic or metal tags on both front flippers and an internal tag (ID-100, Trovan, Ltd., UK) into the left front flipper, or by checking existing tags. Nesting females have been externally tagged since 1985 (Omuta 1997) and internally since 2005 (Yakushima Sea Turtle Research Group 2006). Because female loggerheads lay several clutches of eggs (ca. 110 eggs per clutch [H. Hatase, personal observation]) during a nesting season on the same beaches and remigrate there about every 2 years (Kamezaki et al. 1997; Omuta 1997), a newly tagged female without tag scars was regarded as a recruit and a female tagged in previous years or with tag scars as a remigrant. Although Yakushima Island has several smaller beaches where sea turtles land and nest other than the Inakahama and Maehama beaches, about 80% of landing and nesting by sea turtles at the Yakushima Island are concentrated on these two beaches (Yakushima Sea Turtle Research Group 2009). Some females move between these two and other smaller beaches within and between nesting seasons (Yakushima Sea Turtle Research Group 2009). Thus, there is a possibility that “recruits” at these two beaches contained a few remigrants that had nested at other beaches in previous years. In the present study, the epidermis and eggs of a total of 102 recruits were sampled, which comprised 9.8% of all the recruits in this nesting population in 2008 (Yakushima Sea Turtle Research Group 2009). Straight carapace lengths of all but eight females were measured with calipers. Epidermis samples were sliced from the dorsal side of the neck of turtles with a disposable razor during oviposition (Beauty-M, Kai Razor Co., Ltd, Gifu, Japan) and stored in 100% ethanol at room

temperature. One egg was collected per individual female during oviposition and frozen at -20°C until analytical preparation.

Stable isotope measurements

Stable isotope ratios in egg-yolks were measured following the methods described in Hatase et al. (2002b, 2006). $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ are expressed as deviations from the standard as defined by the following equation:

$$\delta^{13}\text{C} \text{ or } \delta^{15}\text{N} = (R_{\text{sample}}/R_{\text{standard}} - 1) \times 1000(\text{‰})$$

where R is $^{13}\text{C}/^{12}\text{C}$ or $^{15}\text{N}/^{14}\text{N}$. Pee Dee Belemnite (PDB) and atmospheric nitrogen were used as the carbon and nitrogen isotope standards, respectively. The analytical precision was $\leq 0.25\text{‰}$ for $\delta^{13}\text{C}$ and $\leq 0.12\text{‰}$ for $\delta^{15}\text{N}$.

Telomere length measurements

Relative telomere lengths were measured using a real-time PCR method described in Hatase et al. (2008). The amplification of telomeric DNA was compared to the amplification of an endogenous control gene DNA of the same sample and it was expressed as a T/C ratio. We used the 18S ribosomal RNA (rRNA) gene as the control gene. Multiple copies of the 18S rRNA gene exist in a cell (Worton et al. 1988). Normally, single-copy genes such as the 36B4 gene are used as a control gene in relative quantification of telomere length (Cawthon 2002; Callicott and Womack 2006). Although we tried the 36B4 gene as a control gene and reexamined the relationship between age and relative T/C ratios in the epidermis for loggerhead turtles used in Hatase et al. (2008), the result was similar to the published one (H. Hatase et al., unpublished data). We thus adopted the 18S rRNA gene as a control gene. The coefficient of determination for each standard curve was >0.99 . The T/C ratio for each sample was compared to that of a reference standard, and it was expressed as a relative T/C ratio. Real-time PCR was performed three times for each sample, and the mean relative T/C ratio was used in data analysis. If the difference in cycle threshold (Ct) values between duplicates was <0.5 and the differences in Ct values between each of these and another replicate were ≥ 0.5 , the other replicate was omitted as an outlier. Except for the aforementioned case, if the differences in Ct values between triplicates were ≥ 0.4 , the sample was assayed again. The average standard deviation for relative T/C ratios in epidermis samples was 12.5%.

The complete data set on $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ in egg-yolks, straight carapace lengths, and relative T/C ratios in the epidermis for individual loggerhead turtles is available as an appendix (Online Resource 1) in the Electronic Supplementary Material.

Results

Female loggerheads were clearly divided into two groups in a $\delta^{13}\text{C}$ – $\delta^{15}\text{N}$ map (Fig. 1). According to previous findings (Hatase et al. 2002b), 27 females with a $\delta^{13}\text{C}$ of $<-18\text{‰}$ and a $\delta^{15}\text{N}$ of $<12\text{‰}$ in egg-yolks were grouped into oceanic planktivores, whereas 75 females with a $\delta^{13}\text{C}$ of $\geq -18\text{‰}$ or a $\delta^{15}\text{N}$ of $\geq 12\text{‰}$ were grouped into neritic benthivores. The $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ of oceanic foragers ranged from -20.5 to -18.5‰ and 9.2 to 11.9‰ , respectively, whereas those of neritic foragers ranged from -18.5 to -15.5‰ and 12.7 to 18.1‰ (Fig. 1). There were significant differences in straight carapace length between oceanic and neritic foraging groups (*t*-test, $t = 6.461$, $df = 92$, $P < 0.0001$; Fig. 2), with the mean (\pm SD) straight carapace length for oceanic foragers (784 ± 31 mm; range, 739–872 mm; $n = 27$; Fig. 2a) being smaller than that for neritic foragers (840 ± 40 mm; range, 729–925 mm; $n = 67$; Fig. 2b). There were not significant differences in relative T/C ratios in the epidermis between oceanic and neritic foraging groups (*t*-test, $t = 0.829$, $df = 100$, $P = 0.41$), with the mean and median relative T/C ratios in the epidermis for oceanic foragers (mean \pm SD, 1.79 ± 1.37 ; median, 1.44; range, 0.54–7.75; $n = 27$) being slightly larger than those for neritic foragers (mean \pm SD, 1.56 ± 1.13 ; median, 1.43; range, 0.30–9.84; $n = 75$) (Fig. 3).

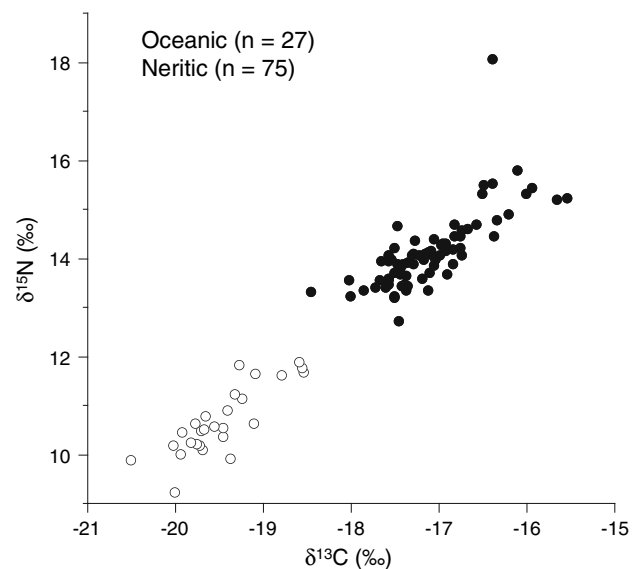


Fig. 1 Plot of the $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values in yolks from eggs that were laid by recruits (first-time nesters) of the loggerhead turtle (*Caretta caretta*) at Yakushima Island, Japan. Turtles with a $\delta^{13}\text{C}$ of $<-18\text{‰}$ and a $\delta^{15}\text{N}$ of $<12\text{‰}$ were regarded as oceanic planktivores, whereas turtles with a $\delta^{13}\text{C}$ of $\geq -18\text{‰}$ or a $\delta^{15}\text{N}$ of $\geq 12\text{‰}$ as neritic benthivores (Hatase et al. 2002b)

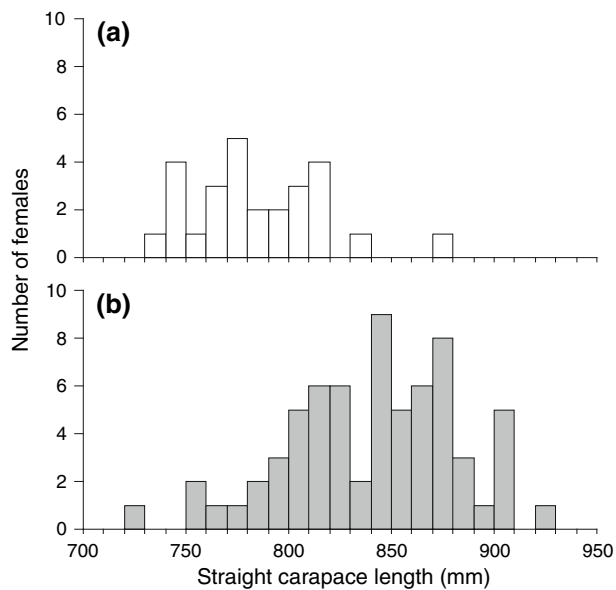


Fig. 2 Size distributions of **a** oceanic ($n = 27$) and **b** neritic ($n = 67$) foraging recruits of the loggerhead turtle. Division of turtles into the two groups is based on $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ in egg-yolks

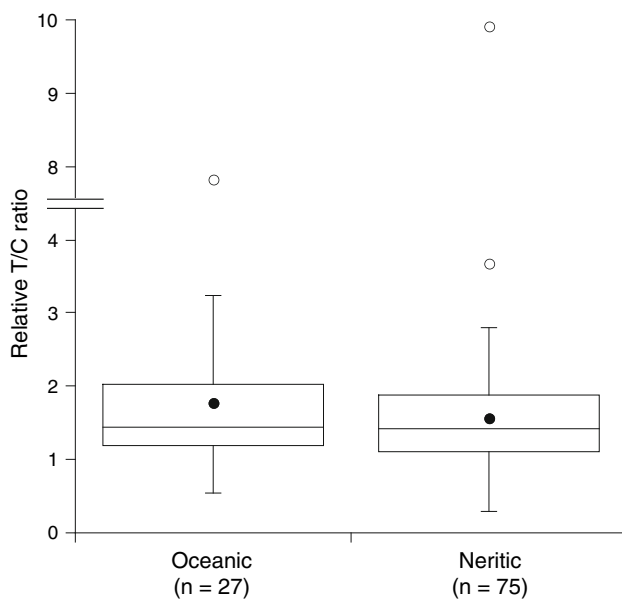


Fig. 3 Telomere lengths (relative telomere to control gene [T/C] ratios) in the epidermis from oceanic and neritic foraging recruits of the loggerhead turtle. Division of turtles into the two groups is based on $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ in egg-yolks. Box, interquartile range of the distribution (25th–75th %); horizontal line within the box, median; solid circle, mean; whiskers, minimum and maximum values; open circle, outlier ($< \text{lower quartile} - 1.5 \times \text{interquartile distance}$ or $> \text{upper quartile} + 1.5 \times \text{interquartile distance}$)

Discussion

This study found that small oceanic-foraging recruits (first-time nesters) of the loggerhead turtle have similar telomere lengths in their epidermis cells to large neritic-foraging

recruits. This suggests that both foraging groups start reproduction at similar ages, which was contrary to our expectation that small oceanic foragers would reach sexual maturity and start reproduction earlier than large neritic foragers (Hatase et al. 2004).

Based on the results obtained in this study, we propose the following scenario that produces and maintains intrapopulation variation in the use of feeding habitats by adult Japanese female loggerhead turtles. After hatching on Japanese beaches, loggerhead turtles migrate to oceanic areas in the central North Pacific along the Kuroshio Current and spend their early lives there (Bowen et al. 1995; Polovina et al. 2004). Faster growing turtles during their oceanic early lives may reach sexual maturity there, whereas others may move from oceanic to neritic areas in the western North Pacific in search of better growth opportunities. In fact, in the western North Atlantic, growth rates of neritic subadults were higher than extrapolated growth rates of oceanic juveniles (Bolten 2003b). Turtles moving to neritic areas may compensate for slow growth during oceanic early lives with accelerated growth by shifting diets from nutrient-poor macroplankton to nutrient-rich benthic animals, as has been seen in some diadromous fishes (Metcalf and Monaghan 2001; Kerr and Secor 2009). Due to this possible compensatory growth, neritic turtles could become larger than oceanic turtles at sexual maturity and start reproduction at similar ages to oceanic ones. Specialization to respective foraging habitats by individual turtles during the adult life stage (Limpus and Limpus 2001; Hatase et al. 2002b; Broderick et al. 2007) may confer a fitness advantage on them through improved foraging efficiency (Bolnick et al. 2003). Intrapopulation variation in habitat use by animals are reported as dispersal polymorphism in insects (e.g. Braendle et al. 2006), partial migration in fishes (e.g. Brodersen et al. 2008), amphibians (e.g. Grayson and Wilbur 2009), birds (e.g. Boyle 2008; Gillis et al. 2008; Ogonowski and Conway 2009), and mammals (e.g. White et al. 2007), facultative diadromy in fishes (e.g. Tsukamoto and Arai 2001), or facultative paedomorphosis in amphibians (e.g. Doyle and Whiteman 2008), and many of these are dependent on environmental conditions. Intrapopulation variation in feeding habitat use by adult female sea turtles may be interpreted within the same framework with the aforementioned phenomena. Indeed, our recent genetic analysis suggested that oceanic and neritic foragers of adult female loggerhead turtles are genetically monomorphic and their foraging dichotomy results from phenotypic plasticity (Watanabe et al. in preparation). Although, in the present study, we only considered a growth condition, mortality risk is another condition that affects ontogenetic habitat shifts by animals (Werner and Gilliam 1984). Future research must address whether the same mechanism with the present study can

explain the variation in habitat use within other conspecific populations (East Atlantic, Hawkes et al. 2006; West Atlantic, Reich et al. 2010) and populations of other sea turtle species (green turtles, Hatase et al. 2006; Seminoff et al. 2008) in order to generalize the mechanisms behind habitat selection by individual sea turtles.

Intrapopulation variation in habitat use leads to alternative life histories. A notion that alternative life histories in adult female loggerhead turtles do not have a genetic basis (Watanabe et al. in preparation) predicts that average fitnesses of the oceanic and neritic groups are unequal (Gross 1996). But in the case of adult Japanese female loggerhead turtles, which life history has a higher fitness? Both oceanic and neritic foragers would start reproduction at similar ages. However, their remigration intervals (the intervals between successive nesting years) are longer than those of neritic foragers perhaps because of the lower energy contents of planktonic prey and the longer migration distances in oceanic habitats (Hatase and Tsukamoto 2008). In addition, remigration intervals and clutch frequencies (the numbers of clutches laid by individual females in a nesting season) for oceanic foragers may vary more than those for neritic foragers because oceanic prey (macroplankton) may fluctuate more with climate and oceanographic processes compared to neritic prey (benthic animals) (Broderick et al. 2001; Saba et al. 2008). Oceanic foragers lay smaller clutches due to their smaller body sizes (Van Buskirk and Crowder 1994). Remigration percentages (survival percentages during the reproductive stage) do not seem to be different between the two groups (Hatase et al. 2004). Summing these up, neritic foragers may have a higher fitness than oceanic foragers. Collection of other life history parameters such as recruitment percentages (survival percentages from eggs to the first reproduction), reproductive longevity, and age-related changes in fecundity is a future subject for accurate comparison of fitness between foraging groups. Altering phenotypes in response to the environment would have allowed sea turtles to maximize fitness and achieve their long evolutionary history.

Acknowledgments We thank the staff and volunteers of the Yakushima Sea Turtle Research Group for field assistance. T. Miyajima of the Marine Biogeochemistry Laboratory, Ocean Research Institute, University of Tokyo, allowed us to use the mass spectrometer. R. Sudo provided technical advice on real-time PCR assay. M. J. Miller helped to improve the manuscript. Two anonymous referees provided constructive comments on the manuscript. This work was partly supported by a grant from the Nippon Foundation to H. H. The experiment was conducted under licenses issued by the municipalities of Kagoshima Prefecture (No. 1-4) and Yakushima Town (No. 230), and in accordance with the Animal Care Authorization (No. P08-1) of the University of Tokyo.

References

- Avens L, Goshe LR (2007) Comparative skeletochronological analysis of Kemp's ridley (*Lepidochelys kempii*) and loggerhead (*Caretta caretta*) humeri and scleral ossicles. *Mar Biol* 152:1309–1317. doi:10.1007/s00227-007-0779-9
- Berthold P (1991) Genetic control of migratory behaviour in birds. *Trends Ecol Evol* 6:254–257. doi:10.1016/0169-5347(91)90072-6
- Bolnick DI, Svanbäck R, Fordyce JA, Yang LH, Davis JM, Hulsey CD, Forister ML (2003) The ecology of individuals: incidence and implications of individual specialization. *Am Nat* 161:1–28. doi:10.1086/343878
- Bolten AB (2003a) Variation in sea turtle life history patterns: neritic vs. oceanic developmental stages. In: Lutz PL, Musick JA, Wyneken J (eds) *The biology of sea turtles. Volume II*. CRC Press, Boca Raton, pp 243–257
- Bolten AB (2003b) Active swimmers–passive drifters: the oceanic juvenile stage of loggerheads in the Atlantic system. In: Bolten AB, Witherington BE (eds) *Loggerhead sea turtles*. Smithsonian Books, Washington, DC, pp 63–78
- Bowen BW, Abreu-Grobois FA, Balazs GH, Kamezaki N, Limpus CJ, Ferl RJ (1995) Trans-Pacific migrations of the loggerhead turtle (*Caretta caretta*) demonstrated with mitochondrial DNA markers. *Proc Natl Acad Sci USA* 92:3731–3734
- Boyle WA (2008) Partial migration in birds: tests of three hypotheses in a tropical lekking frugivore. *J Anim Ecol* 77:1122–1128. doi:10.1111/j.1365-2656.2008.01451.x
- Braendle C, Davis GK, Brisson JA, Stern DL (2006) Wing dimorphism in aphids. *Heredity* 97:192–199. doi:10.1038/sj.hdy.6800863
- Broderick AC, Godley BJ, Hays GC (2001) Trophic status drives interannual variability in nesting numbers of marine turtles. *Proc R Soc B* 268:1481–1487. doi:10.1098/rspb.2001.1695
- Broderick AC, Coyne MS, Fuller WJ, Glen F, Godley BJ (2007) Fidelity and over-wintering of sea turtles. *Proc R Soc B* 274:1533–1538. doi:10.1098/rspb.2007.0211
- Brodersen J, Nilsson PA, Hansson L-A, Skov C, Brönmark C (2008) Condition-dependent individual decision-making determines cyprinid partial migration. *Ecology* 89:1195–1200. doi:10.1890/07-1318.1
- Callicott RJ, Womack JE (2006) Real-time PCR assay for measurement of mouse telomeres. *Comp Med* 56:17–22
- Cawthon RM (2002) Telomere measurement by quantitative PCR. *Nucleic Acids Res* 30:E47. doi:10.1093/nar/30.10.e47
- Denoël M, Joly P, Whiteman HH (2005) Evolutionary ecology of facultative paedomorphosis in newts and salamanders. *Biol Rev* 80:663–671. doi:10.1017/S1464793105006858
- Doyle JM, Whiteman HH (2008) Paedomorphosis in *Ambystoma talpoideum*: effects of initial body size variation and density. *Oecologia* 156:87–94. doi:10.1007/s00442-008-0977-2
- Gillis EA, Green DJ, Middleton HA, Morrissey CA (2008) Life history correlates of alternative migratory strategies in American Dipper. *Ecology* 89:1687–1695. doi:10.1890/07-1122.1
- Grayson KL, Wilbur HM (2009) Sex- and context-dependent migration in a pond-breeding amphibian. *Ecology* 90:306–312. doi:10.1890/08-0935.1
- Gross MR (1996) Alternative reproductive strategies and tactics: diversity within sexes. *Trends Ecol Evol* 11:92–98. doi:10.1016/0169-5347(96)81050-0
- Harrison RG (1980) Dispersal polymorphisms in insects. *Ann Rev Ecol Syst* 11:95–118. doi:10.1146/annurev.es.11.110180.000523
- Hatase H, Tsukamoto K (2008) Smaller longer, larger shorter: energy budget calculations explain intrapopulation variation in

- remigration intervals for loggerhead sea turtles (*Caretta caretta*). *Can J Zool* 86:595–600. doi:10.1139/Z08-035
- Hatase H, Goto K, Sato K, Bando T, Matsuzawa Y, Sakamoto W (2002a) Using annual body size fluctuations to explore potential causes for the decline in a nesting population of the loggerhead turtle *Caretta caretta* at Senri Beach, Japan. *Mar Ecol Prog Ser* 245:299–304. doi:10.3354/meps245299
- Hatase H, Takai N, Matsuzawa Y, Sakamoto W, Omuta K, Goto K, Arai N, Fujiwara T (2002b) Size-related differences in feeding habitat use of adult female loggerhead turtles *Caretta caretta* around Japan determined by stable isotope analyses and satellite telemetry. *Mar Ecol Prog Ser* 233:273–281. doi:10.3354/meps233273
- Hatase H, Matsuzawa Y, Sato K, Bando T, Goto K (2004) Remigration and growth of loggerhead turtles (*Caretta caretta*) nesting on Senri Beach in Minabe, Japan: life-history polymorphism in a sea turtle population. *Mar Biol* 144:807–811. doi:10.1007/s00227-003-1232-3
- Hatase H, Sato K, Yamaguchi M, Takahashi K, Tsukamoto K (2006) Individual variation in feeding habitat use by adult female green sea turtles (*Chelonia mydas*): are they obligately neritic herbivores? *Oecologia* 149:52–64. doi:10.1007/s00442-006-0431-2
- Hatase H, Omuta K, Tsukamoto K (2007) Bottom or midwater: alternative foraging behaviours in adult female loggerhead sea turtles. *J Zool* 273:46–55. doi:10.1111/j.1469-7998.2007.00298.x
- Hatase H, Sudo R, Watanabe KK, Kasugai T, Saito T, Okamoto H, Uchida I, Tsukamoto K (2008) Shorter telomere length with age in the loggerhead turtle: a new hope for live sea turtle age estimation. *Genes Genet Syst* 83:423–426. doi:10.1266/ggs.83.423
- Hawkes LA, Broderick AC, Coyne MS, Godfrey MH, Lopez-Jurado L-F, Lopez-Suarez P, Merino SE, Varo-Cruz N, Godley BJ (2006) Phenotypically linked dichotomy in sea turtle foraging requires multiple conservation approaches. *Curr Biol* 16:990–995. doi:10.1016/j.cub.2006.03.063
- Jonsson B, Jonsson N (1993) Partial migration: niche shift versus sexual maturation in fishes. *Rev Fish Biol Fish* 3:348–365. doi:10.1007/BF00043384
- Kamezaki N, Miyawaki I, Suganuma H, Omuta K, Nakashima Y, Goto K, Sato K, Matsuzawa Y, Samejima M, Ishii M, Iwamoto T (1997) Post-nesting migration of Japanese loggerhead turtle, *Caretta caretta*. *Wildl Conserv Jap* 3:29–39 (in Japanese with English abstract)
- Kerr LA, Secor DH (2009) Bioenergetic trajectories underlying partial migration in Patuxent River (Chesapeake Bay) white perch (*Morone americana*). *Can J Fish Aquat Sci* 66:602–612. doi:10.1139/F09-027
- Limpus CJ, Limpus DJ (2001) The loggerhead turtle, *Caretta caretta*, in Queensland: breeding migrations and fidelity to a warm temperate feeding area. *Chelonian Conserv Biol* 4:142–153
- Lundberg P (1988) The evolution of partial migration in birds. *Trends Ecol Evol* 3:172–175. doi:10.1016/0169-5347(88)90035-3
- Mansfield KL, Saba VS, Keinath JA, Musick JA (2009) Satellite tracking reveals a dichotomy in migration strategies among juvenile loggerhead turtles in the Northwest Atlantic. *Mar Biol* 156:2555–2570. doi:10.1007/s00227-009-1279-x
- McClellan CM, Read AJ (2007) Complexity and variation in loggerhead sea turtle life history. *Biol Lett* 3:592–594. doi:10.1098/rsbl.2007.0355
- Metcalf NB, Monaghan P (2001) Compensation for a bad start: grow now, pay later? *Trends Ecol Evol* 16:254–260. doi:10.1016/S0169-5347(01)02124-3
- Michener RH, Schell DM (1994) Stable isotope ratios as tracers in marine aquatic food webs. In: Lajtha K, Michener RH (eds) *Stable isotopes in ecology and environmental science*. Blackwell, Oxford, pp 138–157
- Miller JD (1997) Reproduction in sea turtles. In: Lutz PL, Musick JA (eds) *The biology of sea turtles*. CRC Press, Boca Raton, pp 51–81
- Monaghan P, Haussmann MF (2006) Do telomere dynamics link lifestyle and lifespan? *Trends Ecol Evol* 21:47–53. doi:10.1016/j.tree.2005.11.007
- Ogonowski MS, Conway CJ (2009) Migratory decisions in birds: extent of genetic versus environmental control. *Oecologia* 161:199–207. doi:10.1007/s00442-009-1356-3
- Olsson IC, Greenberg LA, Bergman E, Wysujack K (2006) Environmentally induced migration: the importance of food. *Ecol Lett* 9:645–651. doi:10.1111/j.1461-0248.2006.00909.x
- Omuta K (1997) *Turtle tracks in Yakushima Island*. Kaiyo Kogaku Kenkyusho Press, Tokyo (in Japanese)
- Polovina JJ, Balazs GH, Howell EA, Parker DM, Seki MP, Dutton PH (2004) Forage and migration habitat of loggerhead (*Caretta caretta*) and olive ridley (*Leptochelys olivacea*) sea turtles in the central North Pacific Ocean. *Fish Oceanogr* 13:36–51. doi:10.1046/j.1365-2419.2003.00270.x
- Reich KJ, Bjørndal KA, Frick MG, Witherington BE, Johnson C, Bolten AB (2010) Polymodal foraging in adult female loggerheads (*Caretta caretta*). *Mar Biol* 157:113–121. doi:10.1007/s00227-009-1300-4
- Saba VS, Shillinger GL, Swithenbank AM, Block BA, Spotila JR, Musick JA, Paladino FV (2008) An oceanographic context for the foraging ecology of eastern Pacific leatherback turtles: consequences of ENSO. *Deep-Sea Res I* 55:646–660. doi:10.1016/j.dsr.2008.02.006
- Seminoff JA, Zárata P, Coyne M, Foley DG, Parker D, Lyon BN, Dutton PH (2008) Post-nesting migrations of Galápagos green turtles *Chelonia mydas* in relation to oceanographic conditions: integrating satellite telemetry with remotely sensed ocean data. *Endang Species Res* 4:57–72. doi:10.3354/esr00066
- Thorpe JE (1986) Age at first maturity in Atlantic salmon, *Salmo salar*: freshwater period influences and conflicts with smolting. *Can Spec Publ Fish Aquat Sci* 89:7–14
- Tsukamoto K, Arai T (2001) Facultative catadromy of the eel *Anguilla japonica* between freshwater and seawater habitats. *Mar Ecol Prog Ser* 220:265–276. doi:10.3354/meps220265
- Van Buskirk J, Crowder LB (1994) Life-history variation in marine turtles. *Copeia* 1994:66–81
- Werner EE, Gilliam JF (1984) The ontogenetic niche and species interactions in size-structured populations. *Ann Rev Ecol Syst* 15:393–425. doi:10.1146/annurev.es.15.110184.002141
- White PL, Davis TL, Barnowe-Meyer KK, Crabtree RL, Garrott RA (2007) Partial migration and philopatry of Yellowstone pronghorn. *Biol Conserv* 135:502–510. doi:10.1016/j.biocon.2006.10.041
- Worton RG, Sutherland J, Sylvester JE, Willard HF, Bodrug S, Dubé I, Duff C, Kean V, Ray PN, Schmickel RD (1988) Human ribosomal RNA genes: orientation of the tandem array and conservation of the 5' end. *Science* 239:64–68. doi:10.1126/science.3336775
- Yakushima Sea Turtle Research Group (2006) Annual report on the landing/nesting of sea turtles at Yakushima Island in 2005. Yakushima Sea Turtle Research Group, Kagoshima (in Japanese)
- Yakushima Sea Turtle Research Group (2009) Annual report on the landing/nesting of sea turtles at Yakushima Island in 2008. Yakushima Sea Turtle Research Group, Kagoshima (in Japanese)