HERPETOLOGICAL JOURNAL, Vol. 12, pp. 115-121 (2002)

BODY MASS CONDITION AND MANAGEMENT OF CAPTIVE EUROPEAN TORTOISES

R. E. WILLEMSEN[1], A. HAILEY[2], S. LONGEPIERRE[3] AND C. GRENOT[3]

[1]*MonteCassinostraat 35, 7002 ER Doetinchem, The Netherlands*

[2]*Department of Zoology, Aristotelian University of Thessaloniki, GR-540 06 Thessaloniki, Greece*

[3]*Ecole Normale Supérieure, Laboratoire d'Ecologie, CNRS-UMR 7625, 46 rue d'Ulm, F-75005 Paris, France*

The condition index (CI) of the tortoises *Testudo graeca, T. hermanni hermanni, T. h. boettgeri* and *T. marginata* was examined in captivity in southern and northern Europe. The CI was calculated using mass-length relationships of wild tortoises: log (M/M'), where M is observed mass and M' is mass predicted from length. The mass-length relationships differed slightly between the subspecies of *T. hermanni*. Captive tortoises at the Centro Carapax (Italy) and the Oosterbeek Tortoise Study Centre (The Netherlands) had CI within the same range as wild tortoises, so there was no general effect of captivity on body mass condition even at densities ten times the highest observed in the wild. However, the seasonal pattern of CI at Oosterbeek differed significantly from that of wild tortoises, with a peak in late summer rather than in spring. Low CI of tortoises in some enclosures at the Centro Carapax prompted supplementary feeding before their health was affected. Tortoises at SOPTOM (France) during a period of disease had significantly lower CI than wild tortoises, with mean CI of -0.04 and mean relative mass (M/M') of 91%. The CI offers a useful guide to the health and management of captive Mediterranean tortoises, although further data are required on those kept in different circumstances, such as outdoor-only enclosures in northern Europe.

Key words: captivity, condition index, management, *Testudo*, tortoise

INTRODUCTION

There are many possible measures of condition in animals, the simplest of which is the body mass condition that compares mass with size (reviewed in Hailey, 2000; Willemsen & Hailey, 2002). A useful condition index (CI) for tortoises is log (M/M'), where M is observed mass, M' is mass predicted from length (L), and M/M' is relative mass (usually expressed as a percentage). Log (M/M') is equal to a residual from a regression of log M on log L. A value of CI=0 indicates that observed mass = predicted mass (i.e. M/M'=1.0 or 100%), whereas a negative value of the CI indicates that observed mass is lower than predicted mass. Previous studies have shown that the CI in wild tortoises varies among species and areas with characteristic seasonal patterns (Willemsen & Hailey, 2002). Veterinary studies have also shown that body mass varies with health (Jackson, 1978, 1980, 1985): a relative mass less than about 80% is an indication of poor health (Hailey, 2000). The veterinary studies cited above used data from captive tortoises to calculate M'. It is not clear whether mass-length relationships of wild tortoises are applicable to captive animals, or whether the latter generally suffer from chronic underweight (e.g. from stress or inadequate food) or obesity (e.g. from inactivity or excessively rich diet).

This paper deals with body mass condition in three large collections of captive tortoises, two in southern Europe and one in northern Europe. The two southern collections were in enclosed natural vegetation near to wild populations, permitting a good test of the effects of captivity (including all the conditions associated with captivity such as social stresses or disease transmission from crowding, diet, and food supply) separate from those of climate and other aspects of habitat. The seasonal variation of the CI in northern Europe, where the climate is less suitable for tortoise activity (Lambert 1981, 1983), was also of interest. We also examine the mass-length relationship in *Testudo hermanni hermanni* (formerly *T. h. robertmertensi*; Bour, 1986). This western subspecies is vulnerable (IUCN, 2000) and susceptible to habitat fragmentation (Longepierre, Hailey & Grenot, 2001) and loss of habitat (Guyot & Clobert, 1997), while the eastern subspecies, *T. h. boettgeri*, is more widespread and abundant (Willemsen & Hailey, 1989) and not currently listed as threatened (IUCN, 2000). Measurement of condition in *T. h. hermanni* is particularly important in view of controversial collection and release programmes (Devaux, 1990) in which large numbers of wild tortoises pass through captivity before relocation. *T. h. hermanni* is thought to differ slightly in shape from *T. h. boettgeri* (Ernst & Barbour, 1989); if the mass-length relationships differ

Correspondence: A. Hailey, School of Biological Sciences, University of Bristol, Woodland Road, Bristol, BS8 1UG. *E-mail*: ah2@ahailey.force9.co.uk

TABLE 1. Details of enclosures, stocking densities and subspecies used to compare body mass condition for captive European tortoises in different study centres: Carapax (Italy); Oosterbeek (The Netherlands); SOPTOM (France).

Centre	Species	No. enclosures	Area (ha)	Density (ha^{-1})	Date of measurements
Carapax	*T. h. hermanni*	2	0.7	170-210	April-May 2000
Carapax	*T. h. boettgeri*	1	0.025	600	April-May 2000
Carapax	*T. marginata*	1	0.7	60	April-May 2000
Carapax	*T. graeca*	2	0.015-0.15	400-1000	April-May 2000
Oosterbeek	*T. h. boettgeri*	1	0.03	1100	April-Oct. 1980, 1985
SOPTOM	*T. h. hermanni*	3	0.03	2000-3300	July-Oct. 1996

significantly, then separate reference equations would be required to calculate M' and the CI in the two subspecies.

METHODS

Wild tortoises were measured in the field as described by Stubbs *et al.* (1984) and released immediately afterwards at the point of capture. Straight carapace length was measured to the nearest 1 mm on a flat-bed scale. The body mass of most tortoises was measured to the nearest 5 g with 2 kg or 3 kg Soehnle spring balances. Small individuals were measured to 1 g with a 250 g Soehnle spring balance. Tortoises in France were measured to 0.01 g on an electronic balance. Sex was determined by plastral concavity and relative tail size; only tortoises larger than 10 cm straight carapace length are considered here. Data were analysed with SPSS and Minitab for regression, analysis of variance (ANOVA) and covariance (ANCOVA), and comparison of a sample mean against an expected value (i.e. CI=0, when mean observed mass = predicted mass) using single-sample t-tests. In ANCOVA we used log M as the dependent variable, log L as the covariate, and sex or subspecies as a fixed factor. The variability of CI values was compared using Bartlett's test of homogeneity of variance (Sokal & Rohlf, 1981). Data on captive tortoises were from three sites and the stocking densities at each site are shown in Table 1.

THE CENTRO CARAPAX, ITALY

Tortoises were housed in enclosures containing their normal habitat of grassland, scrub and open woodland, on a hill slope. CI measurements of *T. h. hermanni* were made in two enclosures with stocking densities of about 200 ha^{-1} (the highest population density found in wild *Testudo* is about 100 ha^{-1}; Stubbs *et al.*, 1985). One enclosure was based on an open field with encroachment of *Rubus*, coarse grasses, and macchia of the oaks *Quercus cerris* and *Q. ilex*, while the other was a former olive grove with *Rubus* scrub. The *T. h. boettgeri* measured here were kept in a grassland enclosure. *T. marginata* were in an enclosure of which a third was oak wood and the rest was olive trees and *Rubus* scrub; this enclosure had been occupied for 10 years and food plants were scarce and even the grass (not usually eaten by *Testudo*) was cropped short. *T. graeca* were kept in different enclosures according to their origin, in vegetation similar to that for *T. h. hermanni*. Natural food plants such as *Medicago*, *Trifolium*, *Rumex*, *Plantago* and various Compositae were reduced in the enclosures due to tortoise grazing. All food plants had been eliminated from the *T. h. boettgeri* enclosure, which contained only grass; these tortoises were fed with fruits and sometimes vegetables (mostly *Lactuca sativa* and *Cichorium andivia*). Captive individuals of *T. h. hermanni, T. h. boettgeri, T. graeca* and *T. marginata* were measured and weighed in the last week of April and the first week of May 2000. Captive *T. h. hermanni* were compared with 159 female and 109 male *T. h. hermanni* from a local, wild population, measured in the same season between 1990 and 1995; several years' data were used to reduce the effect of variation of the CI among years. Each tortoise was considered only once. Further details of Carapax can be found at the web site http://www.novars.it/carapax/.

THE TORTOISE STUDY CENTRE, THE NETHERLANDS

Tortoises were kept out of doors in a large garden at Oosterbeek, with plexiglass domes and a small glasshouse to which the animals had free access for thermoregulation. Their food was growing plants, supplemented with vegetables, fruit and bread. Almost all food plants were natural, or closely related to those eaten in the wild, such as *Trifolium, Sedum, Taraxacum* and *Plantago* species. Tortoises hibernated out of doors, either in natural refuges or in boxes filled with dead leaves or straw. Captive *T. h. boettgeri* were measured and weighed monthly between April and October in 1980 and 1985. A total of 26 tortoises (15 females and 11 males) were measured at different times; each tortoise is considered only once in each month. Further details of the Tortoise Study Centre can be found at the web site http:// www.phys.uu.nl/~eendebak/schild/schild.html.

THE STATION D'OBSERVATION ET DE PROTECTION DES TORTUES DES MAURES (SOPTOM), FRANCE

Tortoises were kept in outdoor enclosures with low scrub of *Cistus* and *Erica*, but few food plants, and were fed vegetables and fruits. Captive *T. h. hermanni* were measured from July to October 1996. Comparative data

TABLE 2. Condition index (CI) of captive European tortoises. *n* is the number of individuals, except at Oosterbeek where this is the number of individual x month observations. *t* is the result of a single sample *t* test with the probability (*P*) that mean CI=0. Females (f) and males (m) are shown separately where there was a significant difference in CI between the sexes.

Group	Location	mean CI	*n*	SD	*t*	*P*
T. h. hermanni	Carapax	-0.0005	99	0.0443	0.12	0.90
T. h. boettgeri	Carapax	0.0177	14	0.0800	0.68	0.51
T. graeca (f)	Carapax	-0.0547	15	0.0407	5.04	<0.001
T. graeca (m)	Carapax	0.0018	9	0.0535	0.09	0.93
T. marginata	Carapax	-0.0229	20	0.0476	2.10	0.047
T. h. boettgeri	Oosterbeek	0.0057	175	0.0391	1.91	0.057
T. h. hermanni	SOPTOM	-0.0421	43	0.0462	5.98	<0.001

from wild tortoises were from Vidauban and Cannet des Maures, Var, France (described by Longepierre & Grenot, 1997) measured from July to October 1997-1999. Each individual was considered only once. Further details of SOPTOM can be found at the web site http://www.tortues.com/index_uk.html.

RESULTS

SUBSPECIFIC DIFFERENCES IN *T. HERMANNI*

The mass-length relationships of wild *T. h. hermanni* in Italy and *T. h. boettgeri* in Greece were compared by ANCOVA of log *M* by subspecies with log *L* as covariate. There was a significant difference between the two subspecies for females ($F_{1,1309}$=10.14, *P*=0.001) but not for males ($F_{1,2054}$=1.66, *P*=0.197), with females being about 3% heavier in Italy than in Greece at the same length. The CI of *T. h. hermanni* was calculated using the mass-length relationships for wild tortoises from Italy. An ANCOVA of log *M* by sex with log *L* as covariate showed a significant difference between the sexes ($F_{1,262}$=14.99, *P*<0.001). Separate reference equations were therefore used for females and males as follows:

Females, Log M = -3.161 + 2.767 log L
(SE intercept=0.108, SE_b=0.050, *n*=156, r^2=95.2%)

Males, Log M = -3.610 + 2.967 log L
(SE intercept=0.238, SE_b=0.114, *n*=109, r^2=86.3%).

The overall standard deviation of the CI was 0.038 (*n*=265). The variability of the CI in wild *T. h. hermanni* was thus identical to that of *T. h. boettgeri* in Greece, which also had SD=0.038 (Willemsen & Hailey, 2002).

CENTRO CARAPAX

The CI of captive *T. h. hermanni* at the Centro Carapax was calculated using the mass-length equations for wild tortoises from Italy (above). The CI did not differ significantly between females and males ($F_{1,97}$=0.009, *P*=0.997). The mean CI for captive tortoises was not significantly different from 0 (Table 2) (this mean is not necessarily equal to 0 because the CI was calculated using the regression for wild, not captive, tortoises). The mean CI for captive tortoises was also not significantly different from the mean CI of wild *T. h. hermanni* in Italy ($F_{1,362}$=0.024, *P*=0.97). Most CI values of captive *T. h. hermanni* at the Centro Carapax were between -0.1 and +0.1 (Fig. 1a), and the variability of CI was similar to that of wild tortoises in Italy (Bartlett's test, χ^2=3.82, df=1, *P*>0.05).

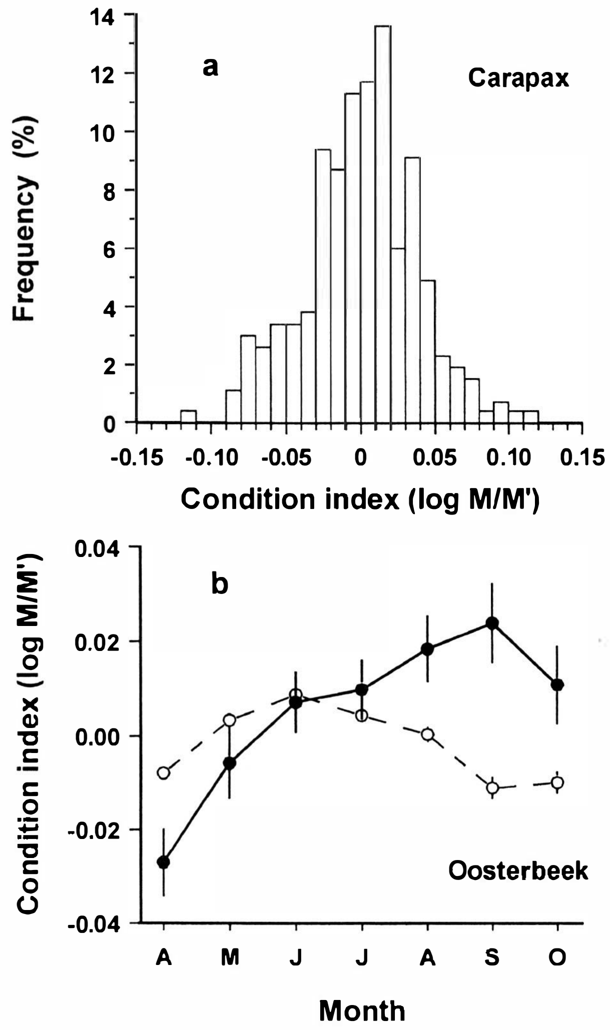

FIG. 1. (a) Frequency distribution of condition index in captive *T. hermanni hermanni* at the Centro Carapax, Italy. (b) Seasonal variation of condition index in *T. hermanni boettgeri;* captive tortoises in Oosterbeek, the Netherlands (solid circles) and wild tortoises in Greece (open circles, from Willemsen & Hailey, 2002). Bars show ± SE.

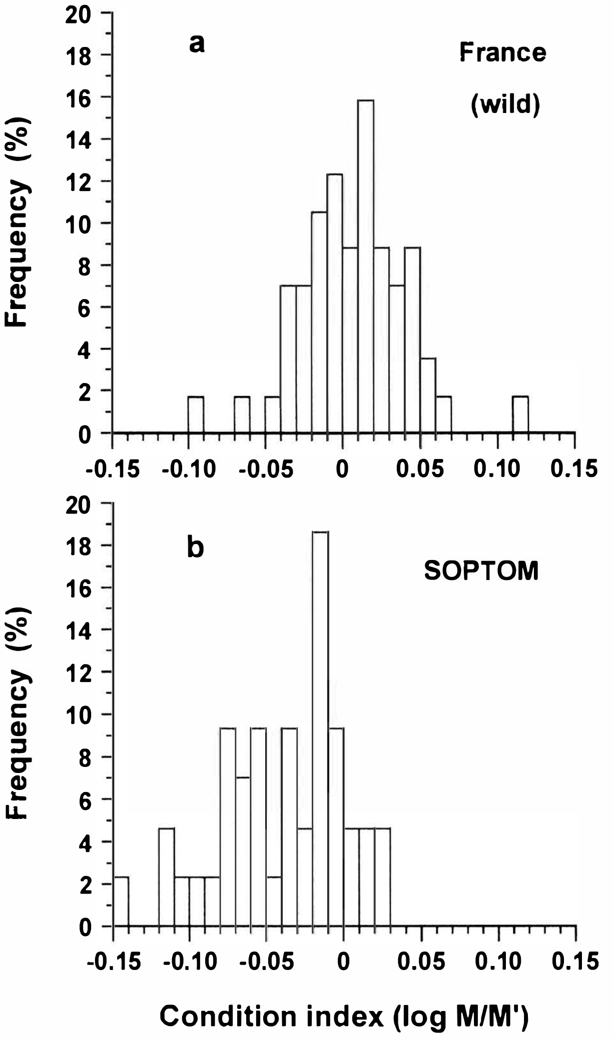

FIG. 2. Frequency distributions of condition index in (a) wild *T. hermanni hermanni* in France, (b) captive *T. h. hermanni* at SOPTOM, France.

There were similar results for captive *T. h. boettgeri* at the Centro Carapax, with CI calculated from the mass-length equations for wild *T. h. boettgeri* from Greece. There was no significant difference between females and males ($F_{1,12}$=0.494, P=0.622), and the mean was not significantly different from 0 (Table 2). The variability of CI of captive *T. h. boettgeri* at the Centro Carapax was, however, significantly greater than that of the captive *T. h. hermanni* (χ^2=10.69, df=1, P<0.01). The greater variability may have resulted from the diverse sources and histories of the non-native tortoises at the Centro Carapax, which were acquired as donations and customs seizures, usually of unknown provenance.

The CI of captive *T. graeca* at the Centro Carapax, calculated using the mass-length equations of wild *T. graeca* (Willemsen & Hailey, 2002), varied significantly with sex ($F_{1,22}$=7.80, P=0.011). The mean CI was significantly different from 0 in females, which had lower mass than predicted, but not in males (Table 2). The CI of captive *T. marginata* at the Centro Carapax, calculated using the mass-length equations of wild *T. marginata*, did not differ significantly between the sexes ($F_{1,18}$=1.45, P=0.244); mean CI was just significantly different from 0 (Table 2), with tortoises having slightly lower mass than predicted.

OOSTERBEEK

The CI of *T. h. boettgeri* in northern Europe was examined in relation to season. A two-way ANOVA of CI with sex and month showed no significant sex × month interaction ($F_{6,161}$=0.21, P=0.973), indicating that the seasonal pattern of CI did not differ between females and males. The seasonal pattern (Fig. 1b) was, however, significantly different from that of wild *T. h. boettgeri* in Greece (Willemsen & Hailey, 2002); two-way ANOVA of CI with status (wild/captive) and month showed a significant interaction of status × month ($F_{6,6185}$=5.82, P<0.001). The CI of the captive tortoises was lower than that of wild *T. h. boettgeri* in April and May, but increased until September, while that of wild tortoises declined after June. Although seasonal patterns of CI differed between wild and captive tortoises, the range of seasonal variation (from about -0.02 to 0.02) was small compared to the total variation. The mean CI at Oosterbeek was not significantly different from 0 (Table 2), and the variability was very similar to that of wild *T. h. boettgeri* in Greece (SD=0.039 and 0.038, respectively).

SOPTOM

The CI of wild *T. h. hermanni* in France was calculated using the mass-length equations for wild *T. h. hermanni* in Italy (above). The CI did not differ significantly between the sexes ($F_{1,55}$=3.64, P=0.062). The mean CI was 0.0026 (n=57, SD=0.0437), not significantly different from 0 (t=0.44, df=56, P=0.66), and most values were between -0.1 and +0.1 (Fig. 2a). The CI of captive *T. h. hermanni* at SOPTOM calculated using the same equations also did not differ between the sexes ($F_{1,41}$=0.51, P=0.480). However, the mean CI at SOPTOM was low, and differed significantly from 0 (Table 2) and from that of wild *T. h. hermanni* in France ($F_{1,98}$=24.4, P<0.001). The frequency distribution of the CI was shifted towards lower values (Fig. 2b), with 10% of observations being below -0.1 compared to about 1% being below -0.1 in other samples (Fig 1a; Hailey, 2000; Willemsen & Hailey, 2002). Nevertheless, the variability of the CI at SOPTOM was similar to that of wild *T. h. hermanni* in France (χ^2=0.15, df=1, P>0.05).

The variability of CI (as measured for example by the SD) is of interest because some putative causes of low mean CI, such as interference competition for food or stress from high aggression, might be expected to increase variation among individuals (with the losers having particularly low values). The variability of CI differed significantly among the seven captive groups described in Table 2 (χ^2=20.20, df=6, P<0.01). The Oosterbeek sample was the least variable; however, this sample included repeated measurements on the same individuals, which would tend to reduce the variability of the data. Nevertheless, the variability of CI differed significantly among the remaining six groups (χ^2=11.98, df=5, P<0.05). The average variability of the CI in all captive tortoises (for comparison with wild populations) was calculated as the weighted (by sample size) mean SD, using the weighted mean variance. The mean SD was 0.044 (calculated from the weighted mean variance).

DISCUSSION

Tortoises in captivity in Italy and in the Netherlands were found to have CI values similar to those in the wild and appeared to be in good health since reproduction was frequent in both centres (R. E. Willemsen, unpublished observations; Eendebak, 1995). Captivity thus does not necessarily lead to a general tendency in *Testudo* (that would be seen in most captive tortoises) to be either underweight or overweight. Spratt (1990) reached a similar conclusion for giant tortoises. Mass-length equations for wild populations may thus be appropriate for calculating the CI of captive tortoises. The western subspecies of *T. hermanni* was slightly heavier than *T. h. boettgeri* at the same length, a difference that corresponds to the more domed shape of *T. h. hermanni* (Ernst & Barbour, 1989). Separate mass-length equations should therefore be used to calculate *M'* in the two subspecies. Most *T. hermanni* in captivity are *T. h. boettgeri,* of which there was previously a large international trade from the Balkans; relatively few *T. h. hermanni* were exported.

The seasonal pattern of CI of *T. h. boettgeri* at Oosterbeek, with maximum values in late summer, was rather different to that in Greece. This pattern supports the hypothesis that while differences in CI among sites in spring are related to activity and thermoregulation, differences in summer and autumn are related to food availability (Willemsen & Hailey, 2002). The peak of CI was thus late at Oosterbeek, continuing a trend observed from southern to northern Greece. The peak did not correspond to the hottest time of year; temperatures in the Netherlands are maximal in July and August, and decline in September (Anonymous, 1996; data for Winterswijk in the eastern Netherlands). High CI in autumn at Oosterbeek was therefore not due to activity/thermoregulation, but probably to food availability. Mediterranean habitats are characterised by dry summers with low food availability in autumn, and low tortoise activity (Hailey & Willemsen, 2000), whereas food and water were always available in captivity. The results at Oosterbeek show that declining CI in autumn is not constant (for example in preparation for hibernation) , but depends on the environment.

Three groups of tortoises had mean CI significantly lower than 0, i.e. body mass on average lower than predicted: *T. marginata* and female *T. graeca* at the Centro Carapax, and *T. h. hermanni* at SOPTOM. The enclosures of *T. graeca* and *T. marginata* at the Centro Carapax were found to have a lack of growing food plants and encroachment of non-edible vegetation. The low CI of the tortoises prompted increased artificial food supply to those enclosures in May 2000. Changing plant species composition is a potential problem for all captive Mediterranean tortoises in enclosures of natural vegetation. Tortoises consume the available food plants, which are not regenerated quickly enough to provide a sustainable food supply and are replaced by less palatable or less edible species. The enclosures may thus continue to have a green and well-vegetated appearance but contain little natural food.

Scarcity of food plants in enclosures also occurred at SOPTOM, but there was also a problem with respiratory disease (Le Garff, 1998; Pieau, 1999). Both herpesviruses and mycoplasmas have been found in captive tortoises at SOPTOM (Fertard, 1997), although the former were mostly associated with *T. graeca.* The mean CI of *T. h. hermanni* at SOPTOM is equivalent to a relative mass of 91%. A similar finding has been reported in the desert tortoise *Gopherus agassizii*: mass-length relationships differed significantly between healthy tortoises and those with upper respiratory tract disease (caused by *Mycoplasma agassizii*), tortoises with clinical signs weighing on average 7% less than those without (Jacobson *et al.*, 1993). Ten percent of captive *T. h. hermanni* at SOPTOM had CI below -0.1, equivalent to a relative mass of 80%, the recommended threshold for veterinary attention (Hailey, 2000). A report from the Société Herpétologique de France has recommended the separation of *T. h. hermanni* enclosures at SOPTOM from those housing *T. graeca* and *T. marginata* (which may be the sources of exotic diseases in French tortoises), and improved monitoring of health (Pieau, 1999). Measurement of CI would be advisable as part of this monitoring.

An additional problem at SOPTOM was the absence of permanent water points in enclosures. Wild *T. h. hermanni* in France travel large distances to find free water when little succulent plant food is available in summer (Longepierre, 2001). Water availability could affect the CI directly through the degree of body hydration, and indirectly through better ability to digest food when water is available. Extensive studies on American *Gopherus* tortoises show the importance of the interaction between food quality, water availability, and energetics (Medica, Bury & Luckenbach, 1980; Turner, Medica & Lyons, 1984; Nagy & Medica, 1986; Henen, 1997; Nagy, Henen & Vyas, 1998; Wallis, Henen & Nagy, 1999). Drinking allows these tortoises to maintain a positive energy balance when feeding on dry plants in summer. This effect of water on digestibility may have contributed to the low CI at SOPTOM (where most measurements were made in late summer, and water was absent), and to the high CI in late summer at Oosterbeek (where water was always readily available) compared to wild *T. h. boettgeri.*

The variability of CI in captive tortoises (overall SD=0.044) was between that of wild *T. hermanni* (SD=0.038) and *T. graeca* (SD=0.039) and that of wild *T. marginata* (SD=0.046) (Willemsen & Hailey, 2002).

There was thus no greatly increased variability of CI in captive populations, even in those groups which had low mean CI (*T. marginata*, female *T. graeca*, and *T. h. hermanni* at SOPTOM). This suggests that captive Mediterranean tortoises do not suffer from aggressive interactions or interference competition for food, which might tend to increase the variability of CI between dominant and subordinate individuals. Such aggressive interactions have often been observed in omnivorous chelonians in captivity (Lardie, 1964; Boice, 1970; Froese & Burghardt, 1974; Boussekey, 1988) and in the wild (Bury & Wolfheim, 1973; Bury, Wolfheim & Luckenbach, 1979; Lovich, 1988). Captive tortoises appear to be less aggressive (Evans & Quaranta, 1949, 1951; Guyot & Lescure, 1994), perhaps because the food of herbivores is less subject to competition in the wild. Aggressive interactions were not observed in captivity during this study.

In conclusion, housing European tortoises in dense groups had no detrimental effect on their body mass condition. Stocking densities ten times greater than the highest population densities in the wild are possible, provided that food and water supplies are adequate and precautions are taken against disease. Further information is needed, however, on the effects of other regimes on the CI and its seasonal variation. Data from non-specialist facilities with fewer tortoises, and from tortoises kept in indoor cages or outdoors in northern Europe without access to glasshouses, would be particularly interesting.

ACKNOWLEDGEMENTS

We thank Donato Ballasina for facilities at the Centro Carapax, the Communità Montana de Colline Metallifere, and Corinne Maag for her hospitality and protection of tortoises in Italy; Bert Eendebak for data on captive tortoises at Oosterbeek, Jacques Thiebaud for help in the field at Centre Var, particularly for the measurements on tortoises, and Clive Cummins and an anonymous referee for useful comments. We also wish to thank the SIVOM of Centre Var and the collective of Cannet des Maures. This study was supported, in part, by the grant DGAD/SRAE No. 96103 from the Ministère de l'Aménagement du Territoire et de l'Environnement.

REFERENCES

Anonymous. (1996). *Tables of temperature, relative humidity, precipitation and sunshine for the world. Part III Europe and the Azores.* London: Meteorological Office.

Boice, R. (1970). Competitive feeding behaviours in captive *Terrapene c. carolina. Animal Behaviour* **18**, 703-710.

Bour, R. (1986). L'identité des tortues terrestres européennes: specimens-types et localités-types. *Revue Francais d'Aquariologie et Herpétologie* **13**, 111-122.

Boussekey, M. (1988). Recherche expérimentale d'etablissement d'une hiérarchie au sein d'un groupe captif de cistudes d'Europe *Emys orbicularis* (Reptilia, Chelonii). *Bulletin de la Société Herpétologique de France* **46**, 1-9.

Bury, R. B. & Wolfheim, J. H. (1973). Aggression in free-living pond turtles (*Clemmys marmorata*). *BioScience* **23**, 659-662.

Bury, R. B., Wolfheim, J. H. & Luckenbach, R. A. (1979). Agonistic behavior in free-living painted turtles (*Chrysemys picta bellii*). *Biology of Behavior* **4**, 227-239.

Devaux, B. (1990). Réintroduction de tortues d'Hermann (*Testudo hermanni hermanni*) dans le massif des Maures. *Revue Ecologie (Terre et Vie) Supplément* **5**, 291-297.

Eendebak, B. T. (1995). Incubation period and sex ratio of Hermann's tortoise, *Testudo hermanni boettgeri. Chelonian Conservation and Biology* **1**, 227-231.

Ernst, C. H. & Barbour, R. W. (1989). *Turtles of the world.* Washington, D.C.: Smithsonian Institution Press.

Evans, L. T. & Quaranta, J. V. (1949). Patterns of cooperative behavior in a herd of 14 giant tortoises at the Bronx Zoo. *Anatomical Record* **105**, 506.

Evans, L. T. & Quaranta, J. V. (1951). A study of the social behavior of a captive herd of giant tortoises. *Zoologica, New York* **36**, 171-181.

Fertard, B. (1997). *Study of tortoise pathology at the Village des Tortues.* Report to the Scientific Council and Board of Directors (In French). Gonfaron: SOPTOM.

Froese, A. D. & Burghardt, G. M. (1974). Food competition in captive juvenile snapping turtles *Chelydra serpentina. Animal Behaviour* **22**, 735-740.

Guyot, G. & Clobert, J. (1997). Conservation measures for a population of Hermann's tortoise *Testudo hermanni* in southern France bisected by a major highway. *Biological Conservation* **79**, 251-256.

Guyot, G. & Lescure, J. (1994). Etude préliminaire du comportement alimentaire en enclos semi-naturel chez la tortue d'Hermann (*Testudo hermanni hermanni* Gmelin, 1789). *Bulletin de la Société Herpétologique de France* **69**, 19-32.

Hailey, A. (2000). Assessing body mass condition in the tortoise *Testudo hermanni. Herpetological Journal* **10**, 57-61.

Hailey, A. & Willemsen, R. E. (2000). Population density and adult sex ratio of the tortoise *Testudo hermanni* in Greece: evidence for intrinsic population regulation. *Journal of Zoology, London* **251**, 325-338.

Henen, B. T. (1997). Seasonal and annual energy budget of female desert tortoises (*Gopherus agassizii*). *Ecology* **78**, 283-296.

IUCN (2000). 2000 *IUCN red list of threatened animals.* Gland: IUCN.

Jackson, O. F. (1978). A method of assessing the health of European and North African tortoises. *British Veterinary Zoological Society* **1978**, 25-26.

Jackson, O. F. (1980). Weight and measurement data on tortoises (*Testudo graeca* and *Testudo hermanni*) and their relationship to health. *Journal of Small Animal Practice* **21**, 409-416.

Jackson, O. F. (1985). The clinical examination of reptiles. In *Reptiles: breeding, behaviour and veterinary aspects*, 91-97. Townson, S. & Lawrence, K. (Eds). London: British Herpetological Society.

Jacobson, E. R., Weinstein, M., Berry, K., Hardenbrook, B., Tomlinson, C. & Freitas, D. (1993). Problems with using weight versus carapace length relationships to assess tortoise health. *Veterinary Record* **132**, 222-223.

Lambert, M. R. K. (1981). Temperature, activity and field sighting in the Mediterranean spur-thighed or common garden tortoise *Testudo graeca*. *Biological Conservation* **21**, 39-54.

Lambert, M. R. K. (1983). Some factors influencing the Moroccan distribution of the western Mediterranean spur-thighed tortoise, *Testudo graeca graeca* L., and those precluding its survival in NW Europe. *Zoological Journal of the Linnean Society* **79**, 149-179.

Lardie, R. L. (1964). Pugnacious behavior in the soft-shell turtle *Trionyx spinifer pallidus* and implications of territoriality. *Herpetologica* **20**, 281-284.

Le Garff, B. (1998). Vie de la Société, VIII. Questions diverses: affaire SOPTOM. *Bulletin de la Société Herpétologique de France* **85-86**, 68-69.

Longepierre, S. (2001). Ecophysiologie de *Testudo hermanni hermanni* Gmelin, 1789: evaluation des contraintes environnementales et alimentaires en milieu naturel dans le sud de la France. Thèse de doctorat. Université Claude Bernard Lyon 1- Ecole Normale Supérieure de Paris.

Longepierre, S. & Grenot, C. (1997). *Distribution de la tortue d'Hermann* (Testudo hermanni hermanni). *Compte-Rendu de l'étude écologique de 10 secteurs dans la Plaine des Maures*. Le Luc: SIVOM du Centre Var.

Longepierre, S., Hailey, A. & Grenot, C. (2001). Home range area in the tortoise *Testudo hermanni* in relation to habitat complexity: implications for conservation of biodiversity. *Biodiversity and Conservation* **10**, 1131-1140.

Lovich, J. (1988). Aggressive basking behavior in eastern painted turtles (*Chrysemys picta picta*). *Herpetologica* **44**, 197-202.

Medica, P. A., Bury, R. B. & Luckenbach, R. (1980). Drinking and construction of water catchments by the desert tortoise, *Gopherus agassizii*, in the Mojave desert. *Herpetologica* **36**, 301-304.

Nagy, K. A., Henen, B. T. & Vyas, D. B. (1998). Nutritional quality of native and introduced food plants of wild desert tortoises. *Journal of Herpetology* **32**, 260-267.

Nagy, K. A. & Medica, P. A. (1986). Physiological ecology of desert tortoises in southern Nevada. *Herpetologica* **42**, 73-92.

Pieau, C. (1999). Affaire S.O.P.T.O.M. .... suite et fin. *Bulletin de la Société Herpétologique de France, Supplément* **90**, 14-17.

Sokal, R. R. & Rohlf, F. J. (1981). *Biometry*. Second edition. San Francisco: W. H. Freeman.

Spratt, D. M. (1990). 'Jackson's ratio' and the Aldabra giant tortoise (*Geochelone gigantea*). *Veterinary Record* **127**, 262-263.

Stubbs, D., Hailey, A., Pulford, E. & Tyler, W. (1984). Population ecology of European tortoises: review of field techniques. *Amphibia-Reptilia* **5**, 57-68.

Stubbs, D., Swingland, I. R., Hailey, A. & Pulford, E. (1985). The ecology of the Mediterranean tortoise *Testudo hermanni* in northern Greece. The effects of a catastrophe on population structure and density. *Biological Conservation* **31**, 125-152.

Turner, F. B., Medica, P. A. & Lyons, C. L. (1984). Reproduction and survival of the desert tortoise (*Scaptochelys agassizii*) in Ivanpah Valley, California. *Copeia* **1984**, 811-820.

Wallis, I. R., Henen, B. T. & Nagy, K. A. (1999). Egg size and annual egg production by female desert tortoises (*Gopherus agassizii*): importance of food abundance, body size, and date of egg shelling. *Journal of Herpetology* **33**, 394-408.

Willemsen, R. E. & Hailey, A. (1989). Status and conservation of tortoises in Greece. *Herpetological Journal* **1**, 315-330.

Willemsen, R. E. & Hailey, A. (1999). Variation of adult body size of the tortoise *Testudo hermanni* in Greece: proximate and ultimate causes. *Journal of Zoology, London* **248**, 379-396.

Willemsen, R. E. & Hailey, A. (2002). Body mass condition in Greek tortoises: regional and interspecific variation. *Herpetological Journal* **12**, 105-114.

Accepted: 10.6.02