

Feeding ecology of the alien invasive pulmonate, *Theba pisana* (White garden snail), in the West Coast National Park, South Africa. T. M.

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ABSTRACT

Theba pisana (White Garden snail), is native to both Southern Europe and Northern Africa, and was introduced to South Africa in 1881. Since then, it has become widely distributed along the coast, including the West Coast National Park (WCNP). This study aimed to determine the feeding ecology (i.e. feeding duration & consumption rate) of *T. pisana*, and thus the impact on the vegetation. Field observations to determine the feeding duration was conducted by observing snails on their naturally occurring vegetation every two-hours for twenty-four-hours over varying weather conditions. Temperature (°C) and humidity (%) were recorded every two hours. Laboratory experiments were performed to determine the consumption rate of five naturally occurring plant species (*Euphorbia mauritanica*, *Chrysanthemoides incana*, *Willdenowia incurvata*, *Ruschia macowanii*, *Lebeckia spinescence*) as well as the cultured diet (cabbage leaves). The results showed that *T. pisana* are inactive in high temperatures (20.4–28 °C), slightly active (10%) in low temperatures (4-8°C) and high humidity (85-96%), and largely active (87-96%) when a constant humidity (49-72%) or sudden moisture (e.g. rain) (56-73%) is experienced irrespective of temperature. Snails preferred cabbage leaves (0.089g/day) to the naturally occurring plant species. With approximately 4.04 snails per m² in the park and snails being active approximately 120 days (i.e. no. of rainy days), the annual potential consumption rate would be 13.5 g/snail on a naturally occurring food item (e.g. *Chrysanthemoides incana* 0.028g/day). With this low density, *T. pisana* might not pose an immediate threat, but the eradication is still important for the continual success of the WCNP as a conservational area.

INTRODUCTION

Very few, if any, ecosystems around the world are without biotic invasions (Mack *et al.* 2000). These biotic invaders are also known as “aliens”, “adventives”, “exotics”, “neophytes” (in the case of plants), “introduced” and “non-indigenous” organisms (Salisbury 1961, Mack 1985, Baker 1986). They occur when organisms are transported to new ecosystems where their descendants proliferate, spread, persist, and very often succeed in becoming potentially harmful pests (Elton 1958).

In the past, the focus of many studies concerning biotic invasions were on the economic losses due to damaged crops (e.g. Baker 1989, Pimentel *et al.* 2001), or running costs of eradication programmes (Van Wilgen *et al.* 2002). As a result, the impacts on indigenous biota are only of recent concern, as studies show the alteration of both terrestrial and aquatic plant and animal communities worldwide. Native species faced with biotic invasions are known to undergo evolutionary changes (e.g. Carrol & Dingle 1996), hybridization (e.g. McMillan & Wilcove 1994), niche displacement (e.g. Race 1982) and extinction (e.g. Rodda *et al.* 1977).

It is thus evident that biotic invasions are becoming increasingly harmful to the Earths biota, and even though many measures of prevention (e.g. quarantine), and control (e.g. chemical and biological) have been established, these organisms persist in almost all areas of the Globe (Mack *et al.* 2000). In the Western Cape, the focus has been largely on the impact of invading alien plants on native vegetation and on water resources (Le Maitre *et al.* 1996 & 2000), alien invasive fish species (e.g. small-mouth bass, *Micropterus dolomieu*; Woodford *et al.* 2005) and marine invertebrates (e.g. the mussel *Mytilus galloprovincialis* and the crab *Carinus maenas*; Robinson *et al.* 2004, 2005). However, the impact of alien invasive terrestrial landsnails found to be potentially harmful elsewhere (e.g. Australia; Baker 1986), has been largely

ignored. This study examines the impacts of *Theba pisana* (White Garden Snail), an agricultural pest in many countries including South Africa (e.g. Baker 1986), in the Western Cape.

T. pisana (Müller) is a native of the Mediterranean regions of Southern Europe and Northern Africa and was introduced into South Africa at the end of the 19th century (Dürr 1946). In its place of origin, *T. pisana* is commonly found on the sand dunes just above the high-water mark (Woodward 1913), as well as in cultivated crops (Gunn 1924). In the Western Cape, the snails have spread rapidly from the coast across the Cape Flats to Gordon's Bay, and also eastward along the seaboard (Dürr 1946). These invasives are thus confined to coastal areas of which Cape Town appears to be one of the most heavily infested. Since their establishment in this area, *T. pisana* have become of economic importance. This is largely due to the snails feeding intensely on vegetable crops and certain species of indigenous shrubs that offer good pasture for livestock (Dürr 1946). The trail of mucus left behind by snails also renders the shrubs unpalatable to the animals (Dürr 1946). *T. pisana* is also thought to be responsible for the local extinction of *Trachycystis rariplacata*, a native snail which occurred at Green Point (Connoll 1916). The city of Cape Town is unfortunately not alone in its infestation of *T. pisana*, as this invasive has become of economic importance in many Mediterranean countries (e.g. Portugal, France, Italy, Algeria and Israel) as well (Baker 1986). Although a popular food in summer, the snails have become severe pests destroying crops (fruit trees and vegetables), and ornamental flowers and shrubs, in many of these countries (Baker 1986). Damages include feeding on flowers, inhibiting pollination of undamaged flowers with slime, blocking harvesters and rendering fouled seeds unmarketable (Baker 1986). Besides being detrimental to the vegetation, *T. pisana* also assists in the dispersal of the

fungus *Colletotrichum lagenarium*, a fungus of melons (Hasan 1976). Studies have also shown that the snail is an intermediate host of the lungworm *Muellerius capillaris* and several other nematodes (e.g. *Neostrongylus linearis*, *Cystocaulus ocreatus*, *Angyostrongylus vasorum*, and *Bronchostrongylus subcretantus*) that can be significant parasites of sheep and cattle (Cabaret 1979, 1982a, Godan 1983).

Many measures of control have been used to eradicate *T. pisana* from areas of invasion. These include manual methods, for example, physical removal of snails from harvests, using rollers for crushing snails, outriggers for knocking snails off the cereal heads, burning, eliminating surface leaf litter, and controlling the growth of vegetation in areas adjacent to crops. Chemicals, for example, Metaldehyde and Methiocarb, have also been used extensively to eradicate *T. pisana*. However, with both mechanical and chemical control, both of which have their own detrimental effects, the invasives are still persistent in affected areas. Biological control (i.e. introducing a pest of the organism) has not yet been tested as a control agent and might be the key to eliminating these pests (Baker 1986).

T. pisana is thus harmful to the economy, as well as the indigenous species of fauna and flora in the areas of the world which it invades. A concerning observation was made in the Western Cape, where this invasive was found in the West Coast National Park (WCNP), a reserve where the main attraction is the diverse flora (C. Griffiths, pers. comm.). As of now, no studies have documented the impact of *T. pisana* within the park. The aim of this study was therefore to establish certain aspects of the feeding ecology of *T. pisana* within the conservation area. Firstly, their feeding duration over 24 hours under various weather conditions was determined. These results, combined with a seasonal weather report of the Langebaan area, would indicate how frequently the weather is suitable for snails to feed. The consumption

rate of various plants on which the snails were observed feeding were also determined. These results, combined with measures of distribution and density being carried out in a sister project, will indicate the extent of damage caused to the flora within the park. The outcome of these two sister projects will hopefully result in a plan of action to eradicate these biotic invaders from the park, as well as from other areas of the Western Cape.

MATERIALS AND METHODS

Study area

The study was conducted at the West Coast National Park (17°57'E; 33°10'S) situated near the town of Langebaan (18°03'E; 33°05'S) in South Africa during two field trips (each approximately three to four days long) in August and September 2006. On both occasions, researchers and volunteers were housed in chalets at the Duine Pos resort within the park. The vegetation is semi-arid fynbos with an annual average monthly rainfall of 278mm (South African Weather service, langebaanweg climate data) (referenced right?) and a hot dry summer (McQuaid *et al.* 1979).

Identification of *T. pisana*

The snails were identified primarily by their colouration. They possess dull subtranslucent white to creamy yellow subglobose shells. The shells are encircled by dark bands of varying colours (i.e. from creamy-yellow to dark purple-brown). The apex of the shell is darker in colour than the rest of the shell and varies from cream to pink-brown in white shells to light brown or purple-brown in banded shells (Connolly 1939, cited in Dürr 1946).

Feeding ecology of *T. pisana* in the field

Diurnal (24-hour) feeding rhythm

The snails, together with the vegetation on which they occurred, were collected within the park and brought back to the chalets. Both snails and vegetation were placed in a bucket filled with soil and left outside for the night to acclimatize. On the first field trip, 100 snails were collected and placed in one bucket and 70 snails in each of two buckets were collected for the second trip. After acclimatization, the proportion of snails observed aestivating and active were recorded every two hours during a 24-hour period. The species of plants being fed on in the buckets were also noted for use in the feeding rate experiments below.

The temperature (°C) and humidity (%) were recorded every two hours using a temperature-hygrometer reader. Because the study was done over a short period of time, observations of the feeding duration under various weather conditions were not possible. For example, very humid conditions in which these snails are reported to be highly active were not experienced (Dürr 1946). An artificial humid climate was thus created by placing a plastic bag pierced with holes (to ensure sufficient ventilation) over one of the buckets, after which the contents were moistened with water using an atomizer every four hours.

Feeding ecology of *T. pisana* in the laboratory

Collection of plants and snails:

Both snails and plants on which the snails were observed feeding on during the feeding duration experiments were brought back to the laboratory at the University of Cape Town. Snails were kept in a temperature of $\pm 20^{\circ}\text{C}$ and maintained in a glass

tank (29.5×23.5 cm) with a section of the lid removed and replaced with net material. Snails were fed at least twice a week on a diet of fresh cabbage leaves.

Consumption rate experiment

Snails of similar sizes (± 10 mm) were starved for 24-hours before the experiment, after which groups of 10 snails were placed in three replicate plastic containers. Within each container, there was a specimen (i.e. stalk and a few leaves/flowers/bulbs) of one of the five plant species (i.e. *Euphorbia mauritanica*, *Chrysanthemoides incana*, *Willdenowia incurvata*, *Ruschia macowanii*, *Lebeckia spinescence*) tested. The experiment was also carried out on cultured food (i.e. cabbage leaves). The three containers without snails served as a control, which was necessary as plants tend to decrease in weight once uprooted due to desiccation and not entirely feeding. To reduce desiccation during the experiment, the plants were kept in a polytop/bottle-top containing water. The specimens of plant material were blotted dry and weighed prior to the experiment using a Mettler PM300 balance. Plants used in the control experiments were of a similar weight to those used in the experimental containers. The containers were compact in size (8.5×6 , 10.5×5.5 , 14.5×4 cm), which allowed the snails to be in relatively close contact with the vegetation. This was important as snails kept in larger containers (28×18 cm) during trial experiments were found aestivating on the sides away from the vegetation. The lids of the containers were pierced with holes for ventilation. To create a humid environment in which the snails are known to be active (Dürr 1946), the caps of the polytops were filled with moist tissue paper and the opening covered with gauze, and these were placed in each container during the experiment. The gauze covering the openings of the polytops were necessary, as snails tended to feed on the tissue paper

during the trial experiments. After 24-hours, both the control and experimental plant material were weighed. The consumption rate was calculated as:

$$\text{Plant material consumed} = (X_{\text{before}} - X_{\text{after}}) -/+ (Y_{\text{before}} - Y_{\text{after}})$$

In which, X: weight of experimental plant material

Y: weight of control plant material

- : when desiccation occurred in control plant material

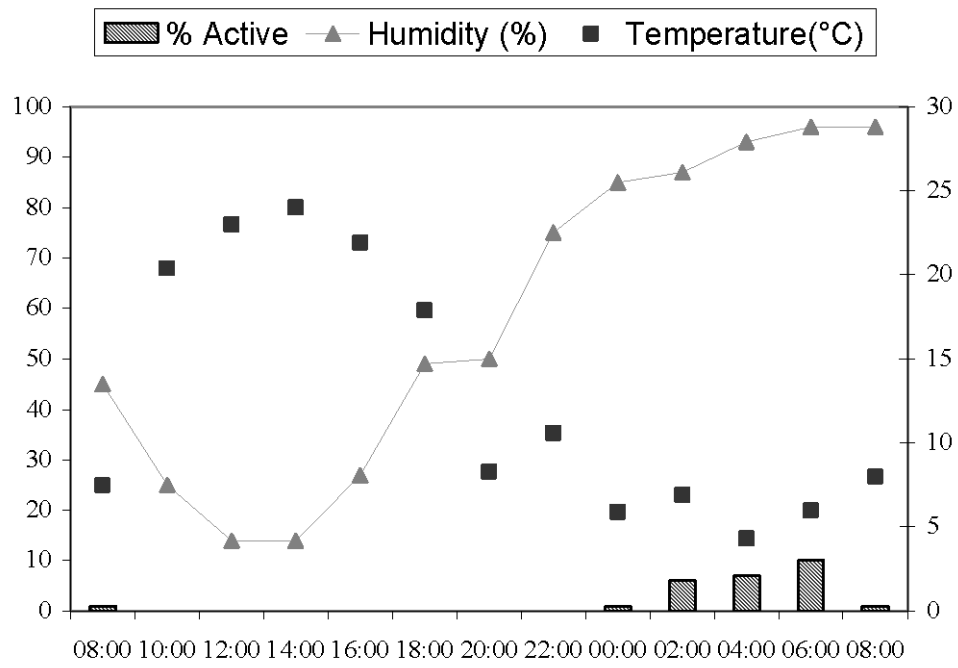
+ : when absorption occurred in control plant material

To determine the amount of food consumed by an individual snail, this amount was divided by the number of snails in each container.

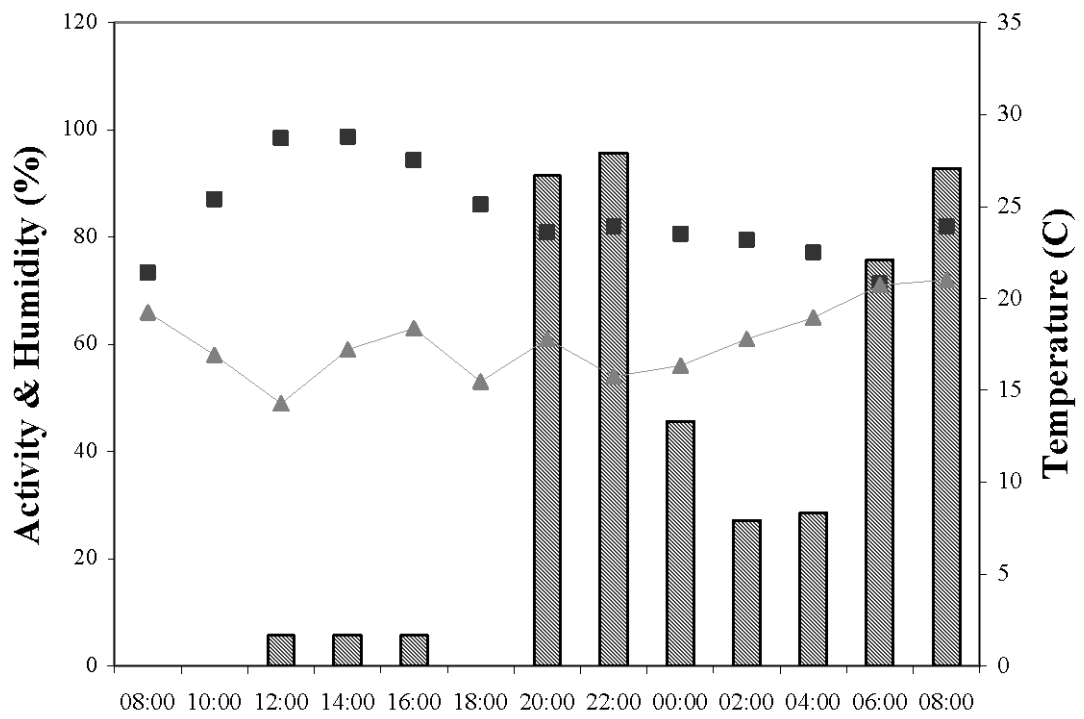
RESULTS

No snails were active during the day and late evening periods (i.e. from 08:00 – 0:00 AM) on the sunny day (Fig. A). Activity started increasing slightly during the early morning periods (i.e. one-ten % from 0:00 – 06:00 AM) when the humidity (%) was highest (85-96%) and the temperature (°C) lowest (4-8°C) (Fig. A). Figure B shows that a relatively high constant humidity (49-72%) results in an increase in the percentage of active snails (i.e. from 6-96%), although the temperature (20.8-28.8°C) remained relatively constant. As was seen during the sunny day (Fig. A), no snails were active during the day and late evening periods (i.e. 08:00 – 0:00 AM) on the cloudy but warm day (Fig. C). A gradual increase (0-87%) in the percentage (%) of active individuals is shown for the early morning periods (i.e. 0:00 – 08:00 AM), when rain was experienced, which resulted in an increase in humidity (56-73%) and a decrease in temperature (23.7-21.3°C).

A



B



C

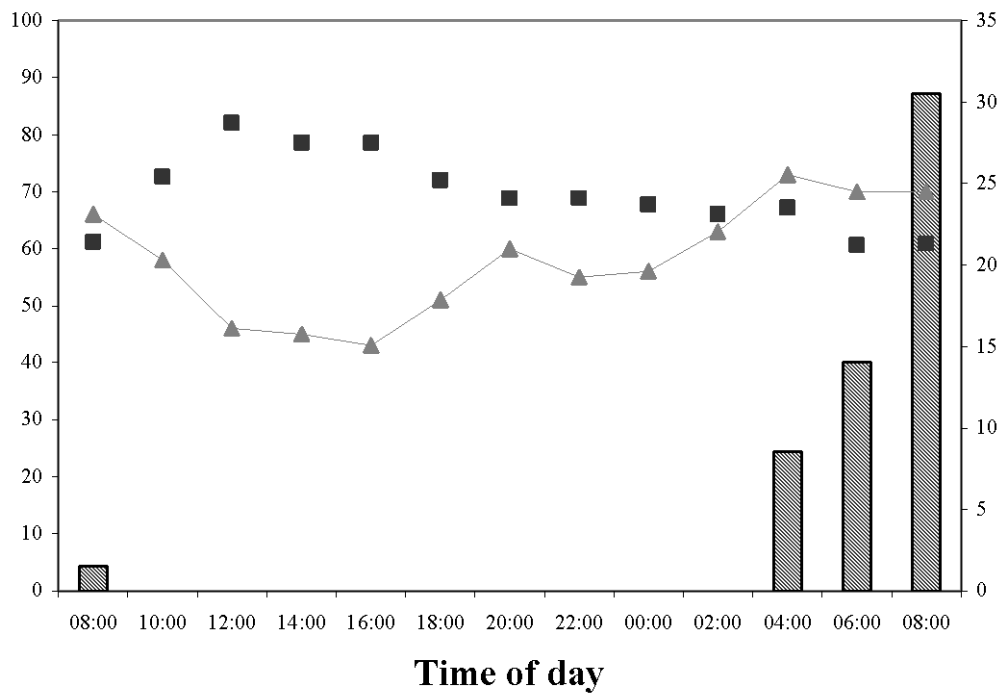


Figure A, B and C. Scatter-plots showing the percentage (%) of active individuals in response to temperature ($^{\circ}\text{C}$) and humidity (%) during a dry-sunny (A), humid (B) and warm-rainy day.

Of the six plant species tested (i.e. including the cabbage leaves), *Chrysanthemoides incana* was the most eaten (i.e. 0.028 ± 0.019 g/day) and *Willdenowia incurvata* was the least eaten (i.e. 0.0003 ± 0.006 g/day) of the naturally occurring vegetation. However, cabbage leaves showed the highest consumption rate (i.e. 0.089 ± 0.058 g/day) of all plant material tested. *Ruschia macowanni* was not consumed at all (i.e. 0.00 ± 0.00 g/day), while *Euphorbia mauritanica* and *Lebeckia spinescence* had similar consumption rates (i.e. 0.009 ± 0.007 and 0.007 ± 0.007

g/day respectively) (Fig. 4).

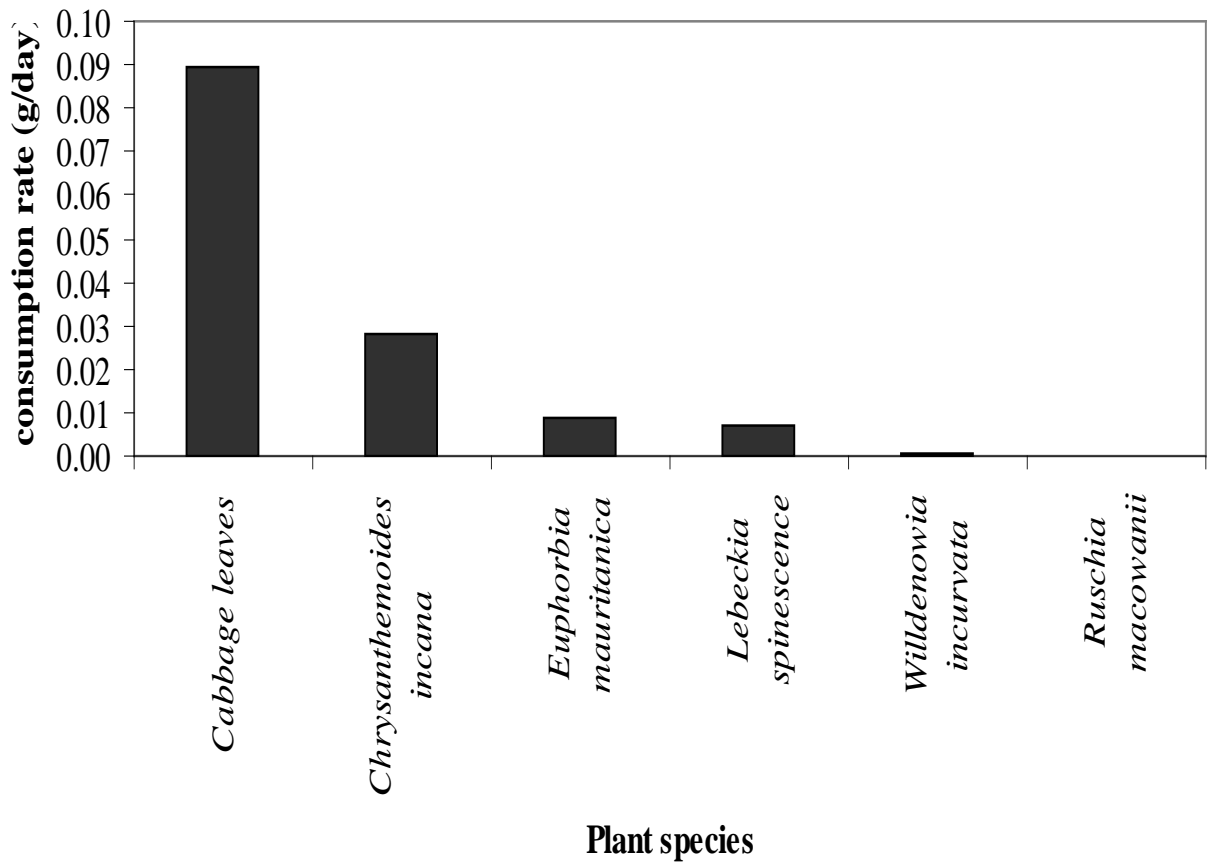


Figure4. Bar graph showing the means (g) and standard deviations of five plant species (i.e. *Euphorbia mauritanica*, *Chrysanthemoides incana*, *Willdenowia incurvata*, *Ruschia macowanii*, *Lebeckia spinescence*), as well as the cultured food (i.e. cabbage leaves).

Table1. Climatological information of the Langebaan area showing the temperature (°C) and precipitation (mm) of monthly averages for the 30-year period between 1961 and 1990 (S. A. Weather Service, 26 October 2006).

Month	Temperature (°C)	Precipitation (mm)
	Average daily maximum	Monthly average
January	28	8
February	28	4
March	27	11
April	25	24
May	21	40
June	19	41
July	18	47
August	19	45
September	20	24
October	23	12
November	25	12
December	26	10
Year	23	278

DISCUSSION

The impact of biotic invasions can be detrimental to both the economy and the natural ecological systems in areas of invasion. Thus, when *T. pisana*, a known pest in many areas of the world, was spotted in the WCNP, an investigation into the impacts of this invasive was required. The conservation area is popular for its diverse flora, thus a study on the impact of *T. pisana* on the vegetation in the park was necessary. The aim of this study was therefore to determine aspects of the feeding ecology of *T. pisana* in the WCNP. The feeding duration in different weather conditions and consumption rate of various plant materials were determined. These results combined with measures of distribution and density being carried out in a sister project, will indicate the extent of damage caused to the flora within the park.

The results showed that no, or very few snails, were active during the day when the temperatures were relatively high (i.e. 20.4 - 23°C and 25.4 – 28 ° C for Fig. 1 and

3 respectively). These results are consistent with those of Dürre (1946), as snails were found to aestivate (summer hibernation) during the daytime, when temperatures were high. In Fig A, activity increased slightly during the early morning periods (i.e. one-ten % from 0:00 – 06:00 AM) when the humidity (%) was highest (85-96%) and the temperature (°C) lowest (4-8°C). A similar result was found by McQuaid *et al.* (1979), where *T. pisana* aroused from aestivation when induced by a combination of low temperatures and high humidity's. For both the warm (Fig. B) and warm-rainy (Fig. C) days, there was a gradual increase in humidity throughout the day, but snails remained inactive. This behaviour was explained by Dürre (1946), who suggested that the temperature limits of activity depends largely on the amount of atmospheric moisture, as a high relative humidity promotes activity. This was shown when a high proportion of snails were active at a temperature of 7 °C and very little at 27.6 °C in the same high relative humidity (i.e. 90-100 %) (Dürre 1946). Thus, as was observed in my study, a gradual increase in humidity will not necessarily result in an increase in activity if temperatures are too high.

However, if a sudden high humidity is experienced, for example, during rain (Fig. C), or when an artificial humid climate was created (Fig. B), *T. pisana* will become active (irrespective of the temperature. These results were consistent with those of Dürre (1946), where it is suggested that moisture influences the activities of *T. pisana* to a great extent, because snails will feed at any atmospheric temperature if moistened with water.

The influence of physical factors on the activity patterns of *T. pisana* is important, as these results combined with a seasonal weather report of the Langebaan area, would indicate whether or not the weather conditions are contributing to the success of the snails as invaders. Climatological information based on monthly

averages for the 30-year period (1961-1990) was collected from the Langebaan area. Using this data (Table 1) together with my results discussed above, I predicted that individuals of *T. pisana* would be mostly active from May to August (i.e. autumn – winter) when temperatures are coolest (i.e. 18°C - 21°C) and precipitation highest (i.e. 40 – 47 mm). The snails will therefore be active for approximately four months of the year. These findings are consistent with that of McQuaid *et al.* (1979), who reported autumn and winter as the seasons in which *T. pisana* is naturally active due to the low temperatures and high humidity's.

The results from the feeding experiments showed that the consumption rate was highest on cabbage leaves, i.e. the cultured food, compared to the vegetation within the park. This is not surprising, as *T. pisana* is a well-known agricultural pest of which green leafy vegetables such as cabbages are preferred. This result was consistent with Dürr (1946), where *T. pisana* also showed a preference for the leaves of plants, especially vegetable crops. Garrison (1993) also reported the tendency of *T. pisana* to feed on tender vegetables of which cabbage was included. This preference for fleshy leaves is also visible when considering the vegetation within the park of which *Chrysanthemoides incana*, a leafy daisy bush, was the most consumed (Fig. 4). Figure 4 also shows that dry-woody plants such as *Willdenowia incurvata* (i.e. a common restio) are not preferred, even though the snails are commonly found on these plants within the park. This result indicates that these plants are used to aestivate on and are not necessarily fed upon by *T. pisana*. This finding is consistent with Chang (1991), whose laboratory feeding preference experiment showed that the land snail *Cepaea nemoralis* rejected plants on which they occur in their natural habitat. These plants are merely used as an escape from the warm ground surface during the day as the snails exhibit a negative geotropic tendency during the daytime (Dürr

1946). This behaviour was also found by Cole (1926), when studying *Helix aspersa*, the brown garden snail. Overall, besides feeding on indigenous vegetation, vegetable crops and the living foliage of many garden and ornamental plants and flowers, *T. pisana* appears to be opportunistic feeders consuming concrete walls and walkways, pulp from weather-wood, paper, tissue paper and prestik (Garrison 1993, personal observations).

The consumption rates for individual snails were calculated as 0.089g/day on cabbage leaves, 0.0003g/day on *Willdenowia incurvata*, 0.028g/day on *Chrysanthemoides incana*, 0.009g/day on *Euphorbia mauritanica* and 0.007g/day on *Lebeckia spinescence*. With approximately 4.04 snails per m² in the park (Odendaal unpublished data) and snails being active for approximately 4 months of the year (i.e. \pm 120 days), the annual potential consumption rate (i.e. consumption rate (g/day) \times density (m²) \times no. of feeding days per year) would be 13.5 g/snail on a preferred food item (e.g. *Chrysanthemoides incana*). It is important to note that these values will only be accurate provided that all 10 individuals within the containers fed during the 24-hour period. Because the snails were not observed during this period, these values are only rough estimates of the consumption rates of *T. pisana*. As not all snails were present on the plants at the end of the experiments (personal observations), there is a high probability that these values apply to far less snails and thus the extent of the damage to the vegetation could be larger.

The high consumption rate on the cabbage leaves is an indicator that the invasives are capable of eating large proportions of vegetation. It is therefore highly probable that the plant species used in the feeding experiments are not their preferred food items within the park. Perhaps *T. pisana*'s preferred food(s) are consumed to such an extent, that these species have been eliminated.

A future study would be to determine the feeding preference of *T. pisana* within the WCNP. This would be carried out via field observations and feeding preference experiments, which were not possible during this project, as no snails were observed feeding naturally within the park. To determine whether their preferred food items are incapable of persisting in the presence of the invasives, one could fence off an area within the park, thus preventing the entry of snails. This would allow for the appearance of plants that might otherwise have been extensively consumed. Another improvement of this project would be to observe the snails (e.g. by using a video recorder) during the 24-hour consumption rate experiments. This would allow for a more accurate estimate of the proportion of food consumed by an individual snail.

The results from both projects have not provided sufficient evidence to prove that *T. pisana* is a potentially harmful pest within the park. The densities of live snails within the park were quite low compared to that outside the park (Odendaal unpublished data) as well as the distribution of *T. pisana* in other areas of invasion (e.g. 39-202 m⁻² in South wales) (Cowie 1984). This could be due to their preference for cultivated crops in the surrounding agricultural areas rather than for naturally occurring vegetation. Nevertheless, eradication of the invasives is still important for the continual success of the WCNP as a conservational area.

REFERENCES

- BAKER, G. H. 1986. The biology and control of White snails (Mollusca: Helicidae), introduced pests in Australia. CSIRO Division of Entomology. Technical paper **25**: 1-31.
- BAKER, H. G. 1989. Patterns of plant invasion in North America. In: *Ecology of Biological Invasions of North America and Hawaii*, (eds) H. A. Mooney & J. A. Drake, p. 44-57. Wiley, New York, New York, USA.
- CABARET, J. 1979. Receptivite experimentale a l'infestation par les larves de protostrongylides de quelques helicides frequents au Maroc. Facteurs de variation. *Ann. Parasitol. Hum. Comp.* **54**: 475-482.
- CABARET, J. 1982a. Polymorphisme de *Euparypha pisana* (Muller) (Mollusca: Pulmonata) et receptivite a l'infestation par les protostrongylides. *Malacologia* **22**: 49-50.
- CARROLL, S. P. & DINGLE, H. 1996. The biology of post-invasion events. *Biological Conservation* **78**: 207-214.
- COLE, W. H. 1926. Geotropism and muscle tension in Helix. *Journal of Genetic Physiology* **8** (3): 253-263.
- CONNOLLY, M. 1916. Notes on the South African non-marine Mollusca. *Annual South African Journal of Mollusca* **13** (5): 187-188.
- DÜRR, H. J. R. 1946. A contribution to the morphology and bionomics of *Theba pisana* (Müller) (Gasteropoda: Helicidae). Department of Agriculture, Union of South Africa. *Science Bulletin* **257**: 1-34.
- ELTON, C. S. 1958. The Ecology of Invasions by Animals and Plants. Methuen, London, UK.

- GODAN, D. 1983. Pest Slugs and Snails. Biology and Control. Springer-Verlag: Berlin.
- GUNN, D. 1924. The brown and grey snails- Two destructive garden pests (*Helix aspera* Müller and *Helix pisana* Müller). *Journal of Department of Agriculture* **9**: 355-362.
- HASAN, S. 1976. Dissemination de champignons phytopathogènes par les gasteropodes. Etude du passage de *Colletotrichum lagenarium* par le tube digestif de *Euparypha pisana*. *Annual Zoology & Ecology of Animals*. **8**: 221-230.
- LE MAITRE, D. C., VAN WILGEN, B. W., CHAPMAN, R. A. & MCKELLY, D. H. 1996. Invasive plants and water resources in the Western Cape Province, South Africa: modelling the consequences of a lack of management. *Journal of Applied Ecology* **33**: 161-172.
- LE MAITRE, D. C., VERSFELD, D. B. & CHAPMAN, R. A. 2000. The impact of invading alien plants on surface water resources in South Africa: A preliminary assessment. *Technical Note* **26 (3)**: 397-408.
- MACK, R. N. 1985. Invading plants: their potential contribution to population biology. In: *Studies on Plant Demography*, (ed) J. White, p.127-142. Academic Press, London, UK.
- MACK, R. N., SIMBERLOFF, D., LONSDALE, W. M., EVANS, H., CLOUT, M. & BAZZAZ, F. A. 2000. Biotic invasions: causes, epidemiology, global consequences, and control. *Ecological Applications* **10 (3)**: 689-710.
- McMILLAN, M. & WILCOVE, D. 1994. Gone but not forgotten: Why have species protected by the Endangered Species Act become extinct? *Endangered Species Update* **11**: 5-6.

- McQUAID, C. D., BRANCH, G. M., FROST, P.G.H.1979. Aestivation behaviour and thermal relations of the pulmonate *Theba pisana* in a semi-arid environment. *Journal of Thermal Biology* **4**: 47-55.
- PIMENTAL, D., MCNAIR, S., JANECKA, J., WIGHTMAN, J., SIMMONDS, C., O'CONNELL, C., WONG, E., RUSSEL, L.ZERN, J. AQUINO, T. & TSOMONDO, T. 2001. Economic and environmental threats of alien plant, animal, and microbe invasions. *Agriculture, Ecosystem and Environment* **84**: 1-20.
- RACE, M. S. 1982. *Oecologica* **54**: 337-347.
- ROBINSON, T.B., GRIFFTHS, C.L. & KRUGER, N. 2004. Distribution and status of marine invasive species in and bordering the West Coast National Park. *Koedoe* **47**: 79-87.
- ROBINSON, T.B., GRIFFTHS, C.L., MCQUAID, C.D. & RIUS, M. 2005. Marine alien species of South Africa- status and impacts. *African Journal of Marine Science* **27**: 297-306.
- RODDA, G. H., FRITTS, T. H. & CHISZAR, D. 1977. The disappearance of Guam's wildlife. *BioScience* **47**: 565-574.
- SALISBURY, E. 1961. Weeds and Aliens. Collins, London, UK.
- VAN WILGEN. B.W., RICHARDSON, D.M., LE MAITRE, D.C. MARAIS, C. & MAGADLELA, D. 2001. The economic consequences of alien plant invasions: examples of impacts and approaches to sustainable management in South Africa. *Environment, Development and Sustainability* **3**: 145-168.
- WOODFORD, D. J., IMPSON, N. D., DAY, J. A. & BILLS, I. R. 2005. The predatory impact of invasive alien small mouth bass, *Micropterus dolomieu*

(Teleostei: Centrarchidae), on indigenous fishes in a Cape Floristic Region mountain stream. *African Journal of Aquatic Science* **30(2)**: 167-173.

WOODWARD, B. B. 1913. The Life of the Mollusca, p.114. Methuen, Ltd., London.