

ASSESSMENT OF PARASITE-MEDIATED SELECTION IN A HOST–PARASITE SYSTEM IN PLANTS

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Abstract. A two-year field study was conducted to evaluate the potential of two cactus species, *Echinopsis chilensis* and *Eulychnia acida*, to evolve defensive traits against the parasitic mistletoe *Tristerix aphyllus* (Loranthaceae). The adaptive value of host traits against parasitism was inferred through: (1) identification of the relevant characters of cacti to prevent infection, (2) evaluation of the fitness impact of parasitism on cacti, and (3) estimation of the linear and nonlinear selection coefficients on the relevant characters. Different lines of experimental and correlative evidence indicated that spine length was important in preventing individuals of the two cactus species from becoming parasitized. However, the impact of the mistletoe on cactus fecundity was contingent on the species involved. Even though parasitism decreased fruit production, seed number per fruit, and the total seed output in *E. chilensis*, low and nonsignificant linear and nonlinear gradients of selection were prevalent in this species, indicating absence of directional and stabilizing/disruptive selection for spine length. Additional analysis based on logistic regression, however, revealed that long-spined *E. chilensis* had a higher probability of reproduction than did short-spined individuals. Unlike its effect on *E. chilensis*, the mistletoe had no fitness impact on *E. acida*, and the maintenance and evolution of spines in this species could not be attributed to parasite-mediated selection. Even though spines act as a first line of defense against parasitism in the two cactus species, selection was detected only on *E. chilensis*. These results indicate that inferences on the adaptive value of host traits based only upon their role in preventing infection run the risk of overestimating parasite-mediated selection, and thus the potential for host–parasite coevolution.

Key words: *Cactaceae; cactus spines; Chile; coevolution; deserts; Loranthaceae; Mediterranean ecosystem; mistletoe; parasite; phenotypic selection.*

INTRODUCTION

Host–parasite relationships have long attracted the attention of ecologists because of suggestions that reciprocal adaptive responses may evolve as a result of the antagonistic interaction (e. g., Price 1980, May and Anderson 1982, Minchella et al. 1985, Toft et al. 1991, Thompson 1994, Yan and Stevens 1995). In spite of its apparent simplicity, this idea has been extremely difficult to evaluate empirically, and coadaptation of host and parasite traits is usually assumed rather than demonstrated. Implicit in most models of host–parasite coevolution is the idea that host characteristics providing defense against parasitism are adaptive and evolve under parasite-mediated selection. However, a rigorous demonstration that a defensive trait is adaptive against parasitism requires, at least, (1) the existence of a functional value for the trait in preventing parasitism, (2) that parasites have a negative impact on host fitness, and (3) that variation in the defensive trait influences host fitness. Although recent methodological advances for the analysis of phenotypic selection offer us a powerful set of tools with which to evaluate this postulate (e. g., Lande and Arnold 1983, Mitchell-Olds and Shaw 1987, Schluter 1988, Phillips and Arnold

1989, Schluter and Nychka 1994), the adaptive value of host traits against parasites has not been previously tested using this perspective. There is an important conceptual distinction between the evolutionary response to natural selection and phenotypic selection. While the evolutionary response to natural selection requires assessment of the genetic change that occurs from one generation to the next, phenotypic selection describes the immediate within-generation effects of natural selection on the statistical distribution of phenotypes, regardless of the genetic basis and inheritance of characters (Lande and Arnold 1983). In this paper I take advantage of this methodology to inquire into the adaptive significance of a putative defensive trait in two sympatric host species against a shared parasite.

Although parasitism by angiosperms is a widespread phenomenon with ~1% of flowering plants being parasitic (Kuijt 1969, Musselman and Press 1995), studies on the evolutionary consequences of parasitism in plant–plant interactions have been only recently initiated (Norton and Carpenter 1998). Most studies assessing adaptive traits in plants have focused on characteristics relevant to seed dispersal (e. g., Jordano 1995), pollination (e. g., Galen 1989, Johnston 1991, Eckhart 1993, Herrera 1993), and herbivory (e. g., Rausher and Simms 1989, Simms and Rausher 1989, Rausher 1992, Nuñez-Farfán and Dirzo 1994, Mauricio

and Rausher 1997). Even though parasitic plants are commonly thought to cause dramatic impacts on host plant fitness, surprisingly few studies have assessed their real impact in natural populations (but see Gómez 1994, Gomes and Fernandes 1994, Silva and Martinez del Río 1996), and therefore the importance of parasite-mediated selection in plants is unknown.

This paper presents the results of a two-year field study on the potential of parasite-mediated phenotypic selection by the mistletoe, *Tristerix aphyllus* (Loranthaceae), on the columnar cacti *Echinopsis chilensis* and *Eulychnia acida* (Cactaceae). The investigation reported here was designed to examine the adaptive value of the spines of cacti in preventing parasitism through evaluation of its role in preventing bird perching and thus seed transmission to cacti. The adaptedness of spines will be inferred through assessment of: (a) the functional role of spines, (b) the impact of *T. aphyllus* on cactus fecundity, and (c) the potential correlation between spine length and cactus fitness. Consideration of these relationships will help elucidate the ecological and evolutionary significance of spines as a defensive trait. More specifically, this study addresses the following questions: (1) Does spine length affect individual susceptibility to infection?; (2) What is the effect of *T. aphyllus* on cactus fecundity?; (3) Does within-population variation in spine length translate into variation in relative fitness? Because all analyses were carried out separately for each host species, it is possible to address comparative questions such as: (4) Do cactus species exhibit similar responses to parasitism, and how comparable is the magnitude, sign and form of the phenotypic selection on spine length? The answers to questions 1–4 relate to the more general one: (5) What is the potential of cacti to evolve adaptations in response to parasitism by *T. aphyllus*?

METHODS

Natural history and study system

Tristerix aphyllus is an unusual leafless holoparasitic mistletoe endemic to the arid and semiarid ecosystems of northern Chile that infects only species of the family Cactaceae (Follman and Mahú 1964, Kuijt 1969, 1988). Unlike most Loranthaceae, this species has leaves that are reduced to minute scales, and the only portion that emerges from the stems of cacti is its red inflorescence. The vegetative portion exists as an endophyte within the tissues of the cacti it parasitizes, and unlike most hemiparasitic mistletoes that tap the xylem of their hosts, *T. aphyllus* parasitizes the phloematic vessels of the cacti (Mauseth et al. 1984, 1985). The fruiting season of the parasitic plant extends from mid–late March to early November, and the peak of fruit production occurs in July–September, depending upon the year. Fruits are single-seeded pseudoberries containing 80% water, that turn from green and red-opaque when unripe to pale pink or translucent white when ripe. Obser-

vations made during three consecutive years indicate that the only bird species responsible for disseminating the seeds of *T. aphyllus* is the Chilean mockingbird *Mimus thenca* (Mimidae). The bird swallows the ripe fruits whole and defecates the seeds intact, no more than three seeds at a time. *Mimus thenca* tends to defend feeding territories and favors the use of some cacti as perches most of the time, which results in large masses of mistletoe seeds being deposited on the cactus columns. Once defecated by *M. thenca*, seeds turn from white to pale brown in 2–3 d, and to red after ~10 d. The naked seeds of *T. aphyllus* are covered entirely by a viscid layer that adheres most of the time to the cuticle and spines of cacti. Seeds germinate within a day after defecation and the bright red radicle grows up to 8 wk or until it makes contact with the epidermis of the cactus. After that, an haustorial plate is developed from which several filaments penetrate into the cactus tissues (Mauseth et al. 1984, 1985).

Echinopsis chilensis and *Eulychnia acida* are columnar cacti that inhabit north-facing slopes in north-central Chile. Their reproduction is relatively synchronous, with the flowering season extending from early September to mid-November, and the fruiting season from mid-October to late December or mid-January. The two cactus species are characterized by broad variability in spine length both within and among populations (Rundel 1976, Hoffmann 1986). Areoles of *E. chilensis* consist of 1–2 long central sclerified spines that project outward, and 8–12 short lateral spines that point in all directions. Areoles of *E. acida* consist of 1–2 long central spines and 10–13 short lateral spines.

This study was conducted from March 1994 to March 1996 in the Reserva Nacional Las Chinchillas (31°30' S, 71°06' W, Aucó, IV Región, Chile), ~300 km north Santiago. The climate is of a semiarid Mediterranean type with most rainfall concentrated in the winter season. Mean annual precipitation is 185.0 mm with large variations from year to year, and frequent droughts (di Castri and Hajek 1976). The total annual precipitation in the Reserve was 43.0 mm in 1994 and 77.1 mm in 1995. The topography of the 4229-ha reserve is rugged and disrupted by several ravines. All measurements were made on populations located on a north-facing slope of Quebrada Torca (slope 25°–30°).

Sampling procedure

I studied 286 individuals (218 *E. chilensis* and 68 *E. acida*) exceeding 1 m in height, including almost every individual present on the slope. Each cactus was tagged with a white plastic plate 14 cm in diameter before the initiation of the seed dispersal season of *T. aphyllus* in 1994. I measured the height of the tallest column of each individual (precision 1 cm), and counted the number of columns exceeding 10 cm in length. Because the bird *M. thenca* tends to perch on the top of columns (Martinez del Río et al. 1995), I calculated a mean spine length from ten apical spines measured

with precision 0.1 mm. The individual status of cacti (parasitized or not parasitized) was recorded at the beginning of the study, and checked periodically for potential emergence of inflorescences of *T. aphyllus*. The parasite load supported by each individual was measured as the number of discrete inflorescences of *T. aphyllus* emerging from the columns of cacti. The activity of *M. thenca* was quantified during 18 d in 1994 and 16 d in 1995, always from sunrise to noon, from a 35° polar-facing slope ~200 m from the plot. This distance proved to be appropriate for recording the identity of the visited cacti as well as the time spent by the bird on each tagged individual. Because the seeds of *T. aphyllus* are white for ~5 d after defecation, turning reddish after 10 d, it was possible to calculate the daily infection rate (DIR hereafter) on each individual by recording the number of white seeds deposited on cacti every 20–25 d, and dividing the total of white seeds recorded in the year by the days comprising the seed dispersal season of each year. This method may underestimate the real DIR but avoids repeated sampling of the same seed over time. The seed dispersal season of *T. aphyllus* comprised 171 d in 1994 and 180 d in 1995. The fruit production of cacti was assessed through monthly censuses during the entire fruiting season. The maximum number of ripe fruits recorded each year was considered to be an estimate of the year's fruit production. This was a reasonable assumption, because most fruits in the same cactus develop in relative synchrony up to maturity. A sample of ripe fruits was removed from cacti and maintained in the laboratory at –20°C prior dissection for seed counting (mean number of fruits removed = 3.43, range: 1–13). I calculated a mean seed number per fruit that allowed estimation of the total seed output per cactus from (fruit production) × (mean seed number per fruit).

Statistical procedure

The number of fruits, number of seeds per fruit, and total seed output were considered as indicative of fitness. Fitness values were normalized to one by dividing individual fitness by the mean fitness of the population. I performed multivariate analysis of phenotypic selection as suggested by Lande (1979) and Lande and Arnold (1983), by considering height, number of columns, and spine length as morphological characters of cacti. I calculated directional (β) and quadratic (γ) selection gradients separately for 1994 and 1995, and for cumulative fitness over the 2 yr. I decided to assess phenotypic selection in separate and cumulative analyses for two reasons. First, patterns of phenotypic selection in plants usually vary among years depending of the selection regime (e. g., Campbell 1989, Schemske and Horvitz 1989, Herrera 1993). Because of high between-year variation in precipitation in the study site, separate annual analyses may help to identify singular selection events attributable to the prevailing selection regime on a year-by-year basis. Second, cumulative reproduc-

tion of long-lived species over years may more realistically reflect differences in maternal fitness than would a series of fitness estimates from different reproductive episodes (Herrera 1993). Because the two approaches provide different perspectives on the same phenomenon, a more complete picture of phenotypic selection may be achieved by performing the two analyses simultaneously. Character values were log-transformed and standardized to have zero mean and unit variance before analysis. This transformation provides standardized selection gradients, thus making comparison of phenotypic selection among years and species possible. β_i represents the average slope of the selection surface in the plane of the character i , and it is computed as the partial regression coefficient in a linear regression of fitness for the character. The magnitude of β_i describes how much standardized fitness changes for a unit change in character i , holding all other characters constant. The sign of β_i indicates the direction of change expected from selection acting directly on character i . For γ , the sign of the coefficient indicates the curvature of the relation between the character and fitness. When the sign is negative, it reflects downward concavity and stabilizing selection influencing the character i . When the sign is positive, it reflects upward concavity and disruptive selection. γ is obtained by regressing standardized fitness on the characters and all pairwise products among characters. In addition to selection gradients, I estimated the opportunity for selection, from the population variance in relative fitness. This coefficient describes the upper limit of the intensity of selection that can act on any character, and allows comparison of the potential of cacti to evolve in response to parasite-mediated selection. Linear and nonlinear standardized selection differentials for spine length were also calculated for each year and for cumulative data. The standardized directional selection differential, s'_i , reflects the extent to which selection shifts the mean of the character i between the actual and potential parents within a generation. s'_i was calculated as s_i/σ_p , where $s_i = \text{Cov}(w, x_i)$, w is the relative fitness, and x_i is the character i . The standardized nonlinear selection differential, C'_i , indicates the standardized change in the variance of character i between actual and potential parents that is attributable to selection, excluding the effects of directional selection. C'_i was calculated as C_i/σ_p^2 , where $C_i = \text{Cov}(w, x_i^2)$.

RESULTS

Effects of spine length on the infection process

Three lines of evidence corroborated the importance of spines as a defensive device against parasitism by *T. aphyllus*. First, the number of visits and the time spent by *M. thenca* perching on cacti were dependent upon spine length in the two cactus species. Except for the number of visits to *Echinopsis chilensis* in 1995, and the time spent on *Eulychnia acida* in the cumulative

TABLE 1. Effect of spine length on the infection process.

Year	<i>Echinopsis chilensis</i>			<i>Eulychnia acida</i>		
	Visits	Time	DIR	Visits	Time	DIR
1994	-0.155*	-0.155*	-0.152*	-0.246*	-0.308*	-0.198*
1995	-0.119†	-0.130*	-0.152*	-0.224*	-0.214*	-0.239*
Pooled	-0.161*	-0.188**	-0.143*	-0.246*	-0.221	-0.244*

Notes: Numbers are standardized partial regression coefficients of spine length on the activity of *M. thenca* and daily infection rate (DIR). Separate multiple regression analyses were performed on each dependent variable using cactus height and number of columns as covariates.

† $P < 0.1$; * $P < 0.05$; ** $P < 0.01$.

data, all partial regression coefficients were negative and significant (Table 1). The negative effect of spines on bird activity translated into a reduced DIR on the long-spined individuals. This result was consistent among years (Table 1). Univariate contrasts for cumulative data revealed that the spines of the unvisited *E. chilensis* and *E. acida* were 1.29 and 2.32 cm longer on the average than spines of the visited individuals (Table 2). Similarly, the spines of *E. chilensis* and *E. acida* without seed deposition were 0.84 and 3.05 cm longer on the average, respectively, than spines of individuals with deposited seeds. Because seed deposition tends to occur on the previously parasitized cacti (Martinez del Rio et al. 1995, 1996), most DIR values were null in the not parasitized individuals (Fig. 1). Pooling cacti in 1-cm spine length intervals allowed comparison of the observed time spent by *M. thenca* perching on cacti against an expected time based on random perching. *Mimus thenca* spent more time than would be predicted by the null expectation in the first intervals of spine length in the two cactus species, showing a reversed trend for longer spines (*G* test, *E. chilensis*: $G = 14\,642$, $df = 8$, $P < 0.001$; *E. acida*: $G = 21\,786$, $df = 7$, $P < 0.001$, Fig. 2). Second, logistic regression of spine length on the presence and absence of *T. aphyllus*, with cactus height and number of columns as covariates, revealed that long spines decrease the probability of *E. chilensis* and *E. acida* being parasitized (model II logistic regression, *E. chilensis*: odds ratio, $OR = 0.813$, $b = -0.207$, $z = 3.035$, $P = 0.007$; *E. acida*: $OR = 0.571$, $b = -0.560$, $z = 2.744$, $P = 0.006$, Fig. 3). Third, in order to test experimentally the correlative evidences described above, in June 1995 I excised the apical spines of 18 *E. chilensis* and 13 *E. acida* leaving only 1–2 cm of each spine. The risk of these cacti receiving seeds of the mistletoe was compared with that of an equivalent number of control cacti

without spine removal, as similar as possible in height and number of columns to experimental individuals. No individual presented external evidence of parasitism by *T. aphyllus* at the beginning of the experiment. Risk was calculated from the ratio (I/N), where I = number of experimental (or control) cacti that received seeds, N = number of experimental (or control) cacti. Tests of the risk ratio among groups were carried out by Stata (1997) software for epidemiological analysis. Individuals were checked for deposited seeds of *T. aphyllus* after 156 d, at the end of the seed dispersal season of *T. aphyllus*. Control individuals of the two species did not receive seeds. Five experimental *E. chilensis*, however, received a total of 15 seeds of *T. aphyllus* (range 1–5), thus indicating a higher risk of becoming infected in comparison to control individuals (experimental = 0.278, control = 0; $\chi^2 = 5.81$, $df = 1$, $P = 0.016$). Although two experimental *E. acida* received a total of 14 seeds, risks did not differ significantly among groups (experimental = 0.154, control = 0, $\chi^2 = 2.17$, $df = 1$, $P = 0.141$). Pooling data from the two species revealed that cacti with excised spines had a higher overall risk becoming infected than did individuals with intact spines (experimental group risk = 0.226, control group risk = 0, $\chi^2 = 7.89$, $df = 1$, $P = 0.005$).

Fitness impact and parasite-mediated selection

Echinopsis chilensis.—Parasite load had a clear and consistent detrimental impact on the fruit production, the seed number per fruit, and the total seed output as revealed by the significant partial regression coefficients, on every fecundity component (Table 3). Cumulative seed output of parasitized individuals was 67.2% lower on the average than for not parasitized cacti (Fig. 4). Regarding the opportunity for selection, *E. chilensis* consistently showed a higher variance than

TABLE 2. Mean spine length (cm; \pm SE) of cacti in relation to bird visits and seed deposition.

Species	Visits by <i>M. thenca</i>			Seed deposition by <i>M. thenca</i>		
	Visited	Not visited	<i>F</i>	Deposited	Not deposited	<i>F</i>
<i>Echinopsis chilensis</i>	10.42 \pm 0.23	11.71 \pm 0.25	14.90***	10.56 \pm 0.26	11.40 \pm 0.19	7.42**
<i>Eulychnia acida</i>	11.86 \pm 0.67	14.18 \pm 0.29	16.83***	10.93 \pm 0.88	13.98 \pm 0.29	16.86***

Note: Degrees of freedom are (1, 217) in *Echinopsis chilensis* and (1, 66) in *Eulychnia acida*.

** $P < 0.01$; *** $P < 0.001$.

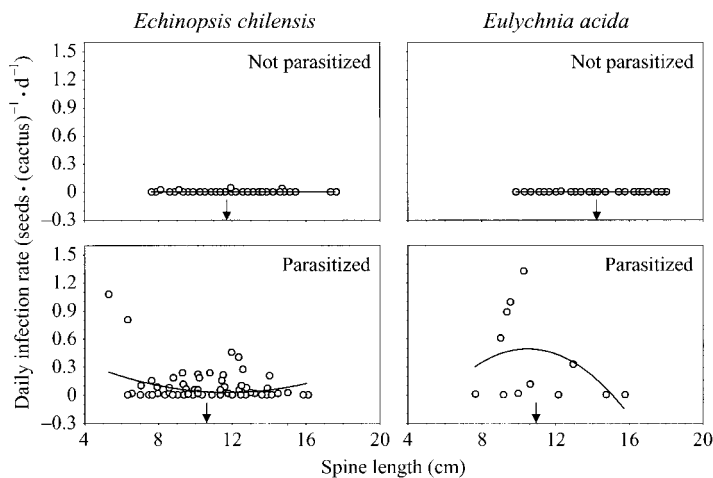


FIG. 1. Associations between spine length and daily infection rate in the parasitized and not parasitized individuals of *Echinopsis chilensis* and *Eulychnia acida*. Arrows indicate mean spine length. Polynomial equations: *E. chilensis* (parasitized): $y = 0.751 - 0.123x$; *E. chilensis* (not parasitized): $y = 0.011 - 0.002x + 0.0001x^2$; *E. acida* (parasitized): $y = -2.086 + 0.492x - 0.023x^2$; *E. acida* (not parasitized): $y = 0.005 - 0.001x$.

E. acida in the seed number per fruit and the seed output fitness components (Table 4). In spite of the high variance in relative fitness, no significant linear (β') and nonlinear (γ') gradients of selection were detected, indicating an absence of directional and stabilizing/disruptive selection on spine length (Table 5). Directional and quadratic regression models accounted for a small amount of the variance in the standardized fitness of *E. chilensis* (range of R^2 , linear model: 0.004%–0.041%, range of R^2 , nonlinear model: 0.012%–0.093%) (Table 5). Similarly, linear and nonlinear standardized differentials were low and nonsignificant, implying that no substantial change in the mean and variance of spine length is expected between actual and potential parents in this species. These results were consistent among years and in cumulative data on every fitness component (Table 5).

Even though parasitism had an important impact on the fecundity of *E. chilensis*, this effect was not translated into statistically significant gradients and differentials of selection. This discrepancy may be explained by the small fraction of the within-population variation in the fecundity of this species that is attributable to *T. aphyllus*. For instance, *T. aphyllus* accounted for 15.5%, 11.4%, and 8.4% of the variation in the cumulative fruit production, seed number per fruit, and seed output, respectively. These figures did not change substantially when data were examined on a yearly basis. However, the absence of effect on the continuous variation of fitness does not necessarily imply that *T. aphyllus* had no impact in suppressing *E. chilensis* reproduction. For instance, systemic parasites such as endophytes, rusts, and smuts often cause complete suppression of reproduction in host plants (see reviews in Clay 1991, Clay and Kover 1996). Because consideration of such a qualitative effect may reveal phenotypic selection otherwise undetectable in least squares regression, I explored such a possibility in more detail by using a generalized linear model in a logistic re-

gression of parasite load and spine length on the presence (1) and absence (0) of reproduction as expected fitness (see Brodie and Janzen 1996). Unlike least squares regression, this procedure may only reveal directional selection, but says nothing regarding nonlinear selection (Price and Boag 1987). The probability of *E. chilensis* becoming reproductive tended to decrease with a unit increment in parasite load (Table 6). These results were consistent among years and in cumulative data. Regarding spine length, positive and significant logistic regression coefficients were observed in 1995 and in the cumulative analysis, indicating that the probability of reproduction increased significantly with a unit increment in the spine length (Table 6). Graphical depiction of cumulative data in *E. chilensis* revealed an asymptotic increase in the probability of reproduction up to a spine length of ~ 12 cm, followed by a slight decrease toward longer spines (Fig. 5).

Eulychnia acida.—Unlike the impact on *Echinopsis chilensis*, *T. aphyllus* had no significant effect on any fecundity component of *E. acida* (Table 3, Fig. 4). Most directional gradients of selection were low and nonsignificant except in 1994, where long-spined cacti produced less fruits than did short-spined individuals (Table 5). Borderline significance was detected for a reduction in fruit production and seed output with increasing spine length (fruits 1995: $\beta' = -0.204$, $t = 1.74$, $P = 0.087$; cumulative fruit data: $\beta' = -0.226$, $t = 1.96$, $P = 0.054$; seeds 1994: $\beta' = -0.206$, $t = 1.77$, $P = 0.082$) (Table 5). The linear regression models for directional selection accounted for a higher fraction of variance in the annual standardized fitness in comparison to *E. chilensis* (range R^2 : 0.159–0.279), and even though the fit was improved in the nonlinear models (range R^2 : 0.255–0.431), all quadratic gradients were nonsignificant, indicating the absence of stabilizing/disruptive selection (Table 5). Most linear and nonlinear selection differentials were statistically significant indicating an important total selection to reduce the mean and var-

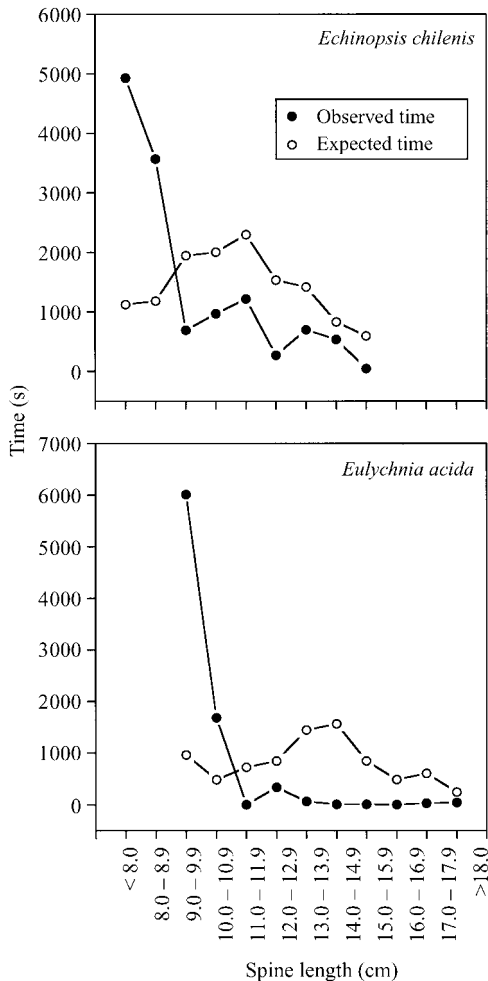


FIG. 2. Observed and expected time spent by *M. thenca* on cacti (1994 and 1995 combined). The observed time on each spine-length interval was calculated by summing the time spent by the bird on every cactus included in the interval. Because intervals included a variable number of individuals, the expected time per interval was estimated from the product between the total time spent by the bird on cacti and the fraction of the total population of cacti included in the interval.

iance of spine length (Table 5). However, because *T. aphyllus* had no impact on *E. acida* fecundity, I cannot suggest parasitism as the factor responsible for the decreasing spine length in this species. No significant logistic regression coefficients were observed, indicating that parasite load and spine length did not affect the probability of individuals becoming reproductive (Table 6).

The absence of impact of *T. aphyllus* on the fecundity of *E. acida* and therefore the lack of significant selection coefficients attributable to parasitism may be explained, in part, by the low frequency of parasitism on this species. A small number of individuals of *E. acida* are parasitized in the Reserve in comparison to *E. chilensis* (mean frequency of parasitism from 10 populations, *E. acida* = 14.7%, *E. chilensis* = 46.6%). Because the parasite prevalence on *E. acida* was 17.6%, it is unlikely that *T. aphyllus* could have a big selective impact on *E. acida* in the study site. Although the question why *E. acida* is less parasitized than *E. chilensis* was not the focus of this paper, it is possible that in comparison to *E. chilensis*, ~2.5 cm-longer spines found in this species represent a more efficient barrier against bird perching (mean spine length [cm] \pm SE, *E. acida*, 13.53 \pm 0.31, *N* = 68; *E. chilensis*, 11.09 \pm 0.15, *N* = 218).

DISCUSSION

Different lines of correlative and experimental evidence indicate that spines were a relevant trait preventing parasitism in *Echinopsis chilensis* and *Eulychnia acida*. Spines influenced the perching behavior of *M. thenca* and therefore the daily infection rate on cacti. The impact of parasitism on cactus fecundity was contingent on the host species involved. While every fecundity component of *E. chilensis* tended to decrease with increasing parasite load, *T. aphyllus* had no demonstrable effect on any fecundity component of *E. acida*. In spite of these differences, parasitism contributed to a small proportion of the within-population variation in the fecundity of the two host species. This resembles conclusions from studies designed to examine the importance of pollinator-mediated selection on floral traits (Herrera 1996). The contribution of pollination to the variance in plant fitness usually does not

FIG. 3. Cubic spline estimate ($\lambda = 100$) of the probability of *Echinopsis chilensis* and *Eulychnia acida* becoming parasitized in relation to spine length. Dots represent raw data values for the presence (1) and absence (0) of reproductive structures of *T. aphyllus* on cacti.

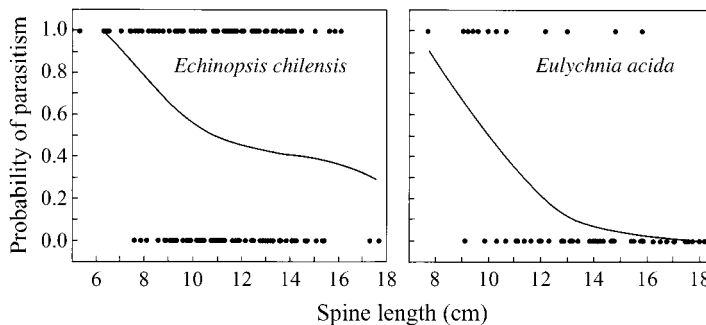


TABLE 3. Impact of parasitism on the fecundity components of *Echinopsis chilensis* and *Eulychnia acida*.

Fecundity component	<i>Echinopsis chilensis</i>			<i>Eulychnia acida</i>		
	1994	1995	Pooled	1994	1995	Pooled
Fruit production	-0.430***	-0.262**	-0.347**	-0.097	-0.069	-0.125
Percentage	5.9	10.9	15.5	0.6	0.7	4.4
Seeds per fruit	-0.423***	-0.260**	-0.325**	-0.068	-0.138	-0.164
Percentage	10.1	10.1	11.4	3.8	5.2	4.8
Seed output	-0.412***	-0.252**	-0.256*	-0.064	-0.122	-0.088
Percentage	9.7	9.3	8.4	3.2	9.8	4.9

Notes: Numbers are standardized partial regression coefficients of the parasite load (number of inflorescence of *T. aphyllus*) on fecundity. Separate multiple regression analyses were performed for each fecundity component per year and for cumulative data using cactus height and number of columns as covariates. Percentage indicates the proportion of the within-population variation in fecundity that is attributable to parasitism. Percentage values were calculated from the variance component in a random effect model.

* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$.

exceed 8% (e.g., Schemske and Horvitz 1988, Herrera 1993), a percentage similar to that documented in this study.

In spite of the higher opportunity for selection shown by *E. chilensis* relative to *E. acida* (Table 4) and the comparable coefficients of variation in spine length among species (*E. chilensis* $cv = 20.5\%$, *E. acida* $cv = 18.7\%$), parasite-mediated selection on *E. chilensis* was only detected in the context of logistic regression as a consequence of the suppression of reproduction in the parasitized and short-spined individuals (Table 6). Because nonsignificant gradients may not only indicate weak selection but also result from a small sample size, I calculated the minimum sample size required to achieve statistical significance at the $\alpha = 0.05$ level as $(t\sigma/\beta)^2$, where β is the gradient of selection, σ is the standard deviation of β , and $t = 1.96$ (Johnston 1991). Results indicated that the minimum sample size for detecting directional selection in pooled data was 1197 individuals in *E. chilensis* (pooled data, $\beta = 1.238$, $\sigma = 21.85$). This implies that increasing sample size in *E. chilensis* may not only reveal phenotypic selection in logistic regression analysis but also in least squares regression.

Unlike *E. chilensis*, phenotypic selection for decreasing spine length in *E. acida* was detected in multivariate linear regression, but not in logistic analysis. The minimum sample size required to detect a significant selection gradient was 68 individuals (pooled data, $\beta = -6.188$, $\sigma = 26.02$), which indicates that the sample size considered in this study was sufficient to detect statistical significance. However, even though the observed selection coefficients are real, improved fit may be achieved by increasing sample size. The reason why spines of *E. acida*, even though functional in preventing infection, tend to evolve toward shorter states is intriguing. Three, not mutually exclusive, potential explanations can account for such phenomenon.

First, it is possible that *T. aphyllus* has a negative fitness impact only in exceptionally dry years, with parasite-mediated selection limited only to a very re-

stricted set of environmental conditions. Parasitic plants may affect host fitness by absorbing resources that are essential for host growth and reproduction. However, the way hosts are affected may depend not only on how much of their resources are captured by parasites but also upon the supply available in the environment, which may constrain the evolutionary

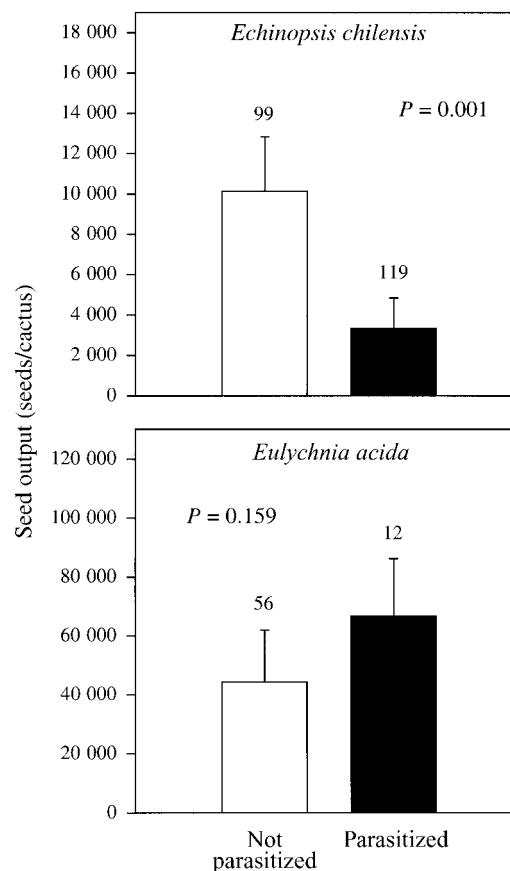


FIG. 4. Mean seed output of parasitized and not parasitized individuals of *Echinopsis chilensis* ($F = 10.88$) and *Eulychnia acida* ($F = 2.03$) in 1994 and 1995. Bars represent 1 SE.

TABLE 4. Opportunity for selection (variance in relative fitness) in *Echinopsis chilensis* and *Eulychnia acida*.

Year	Fitness component	<i>E. chilensis</i>	<i>E. acida</i>	<i>F</i>
1994	Fruit production	5.69	5.07	1.12
	Seeds per fruit	6.60	0.99	6.64***
	Seed output	11.36	5.63	2.02***
1995	Fruit production	4.92	5.97	0.82
	Seeds per fruit	6.94	1.29	5.40***
	Seed output	11.78	6.04	1.95***
Pooled	Fruit production	3.76	5.51	0.68†
	Seeds per fruit	4.94	0.67	7.32***
	Seed output	11.59	6.53	1.77**

Note: *F* values result from Bartlett's test for homogeneity of variance.

† $P < 0.1$; * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$.

response of the plant hosts. Water availability is an obvious factor affecting the fecundity of cacti (Gulmon et al. 1979, Gibson and Nobel 1986, Silva and Acevedo 1995). Even though cacti are better protected against desiccation than most other plants in arid and semiarid zones, availability of summer water often sets limits to photosynthesis which may ultimately translate into limitations in fruit and seed production (Mooney 1983, Lechowicz 1984, Tenhunen et al. 1985). Because *T. aphyllus* represents a sink for water and inorganic carbon nutrients otherwise available to cacti, its contribution to the population variation in cactus fecundity may be contingent on the water availability in the study site. Moreover, long-lasting droughts and short pulses of high precipitation define the between-year climatic conditions in north-central Chile as a consequence of El Niño events (di Castri and Hajek 1976, Ortlieb 1994). If current fitness of cacti comes from resources stored in past years, then current phenotypic selection may not necessarily reflect the prevailing selective regime imposed by *T. aphyllus*, but rather the environmental conditions of previous years.

Second, long spines may be a consequence of parasite-mediated selection that occurred in the past under more stringent conditions for cacti, but are unnecessary

at present due to the lack of impact of *T. aphyllus* on cactus fecundity. The last important glacial period in semiarid Chile ended ~14 000 years ago (Mercer 1972), followed by an intense warming trend at the Pleistocene/Holocene transition that culminated ~6500 years ago, when temperatures were at least 1°–3°C above current values (Solbrig et al. 1977, Ortlieb et al. 1996, Veit 1996). Current spine length in *E. acida* may thus represent the product of intense selection that occurred in the past rather than in present conditions. The lack of adaptive value of long spines in *E. acida* suggests this trait might be better considered anachronistic to parasitism, if demonstration of its adaptive value against parasitism in the past is provided. In the same vein, herbivory may also be invoked as responsible for the evolution of cactus spines. Janzen (1986) suggested that herbivorous species were the main selective agents for the evolution of spines in nopaleras (*Opuntia*). It is possible that the spine length shown by *E. acida* at present evolved as a defensive device against a Chilean megafauna that disappeared around the late Pleistocene (Marshall 1981). These two "anachronism" hypotheses, although difficult to test unequivocally, advocate not only a lack of adaptation of spines to parasitism but also a cost of maintenance for long-spined individuals. The absence of impact of *T. aphyllus* on the fecundity of *E. acida* suggests that the maintenance of long spines may represent an unnecessary or even maladaptive investment of resources that otherwise could be allocated to growth and reproduction. It is known that investment in defense against herbivory and pathogens represents an important component of the lifetime resource budget of plants (Bazzaz et al. 1987). Most models of the evolution of resistance assume that defensive traits have a fitness cost, because the production and maintenance of such structures often demands energy that could be used for vegetative or reproductive tissue (e. g., Gulmon and Mooney 1986, Fagerström et al. 1987, Simms and Rausher 1987). Although fitness costs have been demonstrated in a variety of species (e. g., Coley et al. 1985, Coley 1986,

TABLE 5. Gradients and differentials of selection for spine length (cm) in *Echinopsis chilensis* and *Eulychnia acida*.

Year	Fitness component	<i>Echinopsis chilensis</i>			<i>Eulychnia acida</i>		
		β'	<i>S'</i>	<i>C'</i>	β'	<i>S'</i>	<i>C'</i>
1994	Fruit production	0.050	-0.048	-0.761	-0.237*	-0.815**	-8.045**
	Seeds per fruit	0.022	-0.059	-0.935	-0.031	-0.159	-1.749
	Seed output	0.086	0.046	0.007	-0.206†	-0.785**	-7.716*
1995	Fruit production	0.027	0.062	0.366	-0.204†	-0.800**	-7.911*
	Seeds per fruit	0.065	0.177	1.704	0.146	-0.025	-0.339
	Seed output	-0.002	-0.019	-0.373	-0.135	-0.656*	-6.954*
Pooled	Fruit production	0.059	0.068	0.393	-0.226†	-0.826**	-8.138**
	Seeds per fruit	0.051	0.060	0.397	0.082	-0.096	-1.082
	Seed output	-0.009	-0.094	-1.296	-0.178	-0.778**	-7.627*

Notes: β' indicates standardized directional gradients of selection; *S'* and *C'* indicate standardized linear and nonlinear differentials of total selection, respectively. *P* values for selection differentials were calculated from Pearson's product-moment correlation.

† $P < 0.1$; * $P < 0.05$; ** $P < 0.01$.

TABLE 6. Logistic regression coefficients (\pm SE) of parasite load and spine length (cm) on the cumulative probability of cacti becoming reproductive.

Species	Variable	Coefficient	Odds ratio	z
<i>Echinopsis chilensis</i>	Parasite load	-0.038 ± 0.009	0.963	4.34***
	Spine length	0.151 ± 0.066	1.163	2.30*
<i>Eulychnia acida</i>	Parasite load	-0.061 ± 0.054	0.941	1.13
	Spine length	-0.164 ± 0.170	0.848	0.96

Notes: Cactus height (m) and number of columns were used as covariates in analyses. P levels were estimated from Wald's test.

* $P < 0.05$; *** $P < 0.001$.

Simms and Rausher 1989, Ågren and Schemske 1993), it is becoming increasingly clear that allocation of resources to defense is expected to occur until the benefit of investment becomes limited by costs (e. g., Sagers and Coley 1995, Mauricio and Rausher 1997, Mauricio 1998).

Third, long spines in *E. acida* may result from phylogenetic inertia rather than having evolved by natural selection for its defensive function. Although questions pertaining to the origin of the character can be better assessed by phylogenetic studies of adaptation (Reeve and Sherman 1993, Losos 1994, Larson and Losos 1996), spines perform important physiological functions in cacti. For example, they protect the stems from damaging wavelengths of solar radiation (Gibson and Nobel 1986) and also create a boundary layer between stems and the external environment that reduces evapotranspiration as well as the risks of overheating and freezing damage from extreme temperatures (Nobel 1978, Gibson and Nobel 1986, Nobel 1988). Although I cannot rule out the importance of these abiotic factors for the evolution of spines in cacti, such hypotheses are more concerned with the original adaptive value of spines rather than with their

co-opted functional role to prevent parasitism (exaptations in the terminology of Gould and Vrba 1982, Reeve and Sherman 1993). Because spines of *E. acida* are significantly longer than those exhibited by non-parasitized congeneric species (R. Medel, unpublished data), it is unlikely that actual spines result from phylogenetic inertia.

In this paper I assessed the potential of two cactus species to evolve adaptations under parasite-mediated selection. The adaptive value of spines against parasitism was inferred through examination of the following three conditions: (a) the importance of spines in preventing infection, (b) the impact of parasitism on cactus fecundity, and (c) correlation among spine length and relative fitness. Results from this study revealed a picture far more complex than previously thought. The adaptedness of spines was not similar in the two host species, and conclusions about parasite-mediated selection are necessarily contingent upon the host species involved. Even though different lines of evidence indicate that spines prevented infection in *E. chilensis* and *E. acida* (condition "a" verified for the two cactus species), *T. aphyllus* had a detrimental impact only on the fecundity of *E. chilensis* (condition "b" verified for *E. chilensis* but not for *E. acida*). While parasite-mediated selection on the relative fitness could not be detected, suppression of reproduction attributable to parasitism, and thus parasite-mediated selection for long spine length was observed in *E. chilensis* (condition "c" verified for *E. chilensis* but not for *E. acida*). But why, if spines are important to prevent infection in *E. acida*, are they not only inconsequential in terms of fitness advantage but even maladaptive at present? The answer to this question may require a long-term study where the various environmental factors that directly and indirectly affect the impact of parasites on host fitness can be quantified during several host reproductive events. The extent to which parasite-mediated selection on cacti varies over time needs to be assessed in future studies. In the absence of such information, inferences on the adaptive value of host traits against parasitism that rest only upon their ecological function to prevent infection may ignore the real evolutionary significance of host characters, and thus may lead to

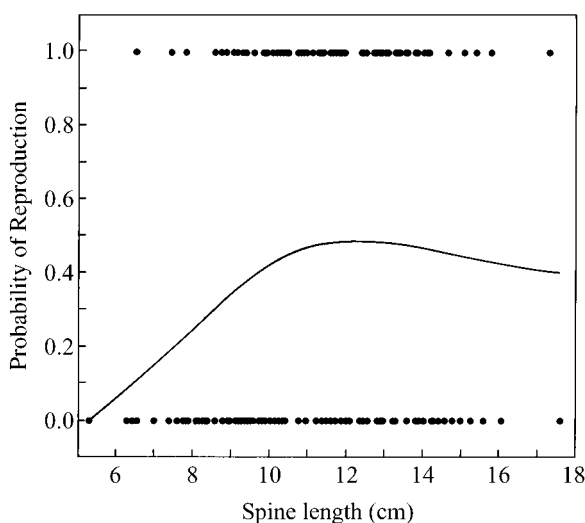


FIG. 5. Cubic spline estimate ($\lambda = 100$) of the fitness function for *Echinopsis chilensis* in relation to spine length. Dots represent raw data values for the cumulative probability of reproduction (1), and absence of reproduction (0).

erroneous conclusions about host-parasite coevolution.

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