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Determinants of vigilance in a reintroduced population of Père David's deer

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Abstract After being kept in captivity and isolated from natural predators for more than 1,200 years, Père David's deer has been reintroduced in China and now occurs in a reserve where human activity is the only potential threat. Antipredator vigilance is an important component of survival for many prey animals in their natural habitat. Do deer still adjust vigilance as a function of risk after such a long period of relaxed predation pressure? Here, we examined vigilance levels in Père David's deer groups as a function of group size, sex and level of human disturbance. The results showed that individual vigilance significantly decreased with group size in all-female groups but not in all-males or mixed-sex groups. In rutting season, males compete with one another and harass females, and we argue that vigilance is partly aimed at threatening males and that such vigilance increases with group size. This explains why overall vigilance did not vary with group size for males in general and for females in mixed-sex groups. Vigilance increased in more disturbed areas but in in male deer only. The results indicate that despite relaxed predation pressure over centuries, Père David's deer can still adjust antipredator responses as a function of perceived risk. Such information may become useful in the rewilding programme now under way for this species in China [*Current Zoology* 59 (2): 265–270, 2013].

Keywords Antipredator vigilance, Group size, Human disturbance, Sexual competition, Père David's deer

Père David's deer *Elaphurus davidianus*, a large ruminant, is one of a handful of species that has been extirpated from its natural habitat but survives in captivity (Jiang et al., 2000). This deer species, which naturally occurred throughout eastern Asia, is thought to have disappeared from the wild nearly 1200 years ago, and has been held in captive groups ever since. The species was reintroduced in China in 1986 from a captive herd held in England (Li et al., 2007). While many predators such as tiger *Panthera tigris* and wolf *Canis lupus* are believed to have preyed upon Père David's deer in its natural habitat, no direct experience with predators has probably occurred for several centuries (Li et al., 2011). Do deer retain any antipredator behavior after such a long absence of interactions with their predators? For instance, do they still recognize sights and sounds of their former predators or do they still adjust antipredator vigilance as a function of predation risk? Knowledge about such responses to potential threats is crucial to a reintroduction programme since relearning to avoid predators may be necessary for species that have lost appropriate responses (Griffin et al., 2000).

Relaxed predation pressure in the recent evolutionary history of a species can have contrasting effects (Lahti et al., 2009). Some species have retained antipredator responses over thousands of years after relaxed selection (Byers, 1997; Placyk and Burghardt, 2011) while other species show degraded responses after just a few decades or centuries (Berger et al., 2001; Blumstein and Daniel 2002; Blumstein et al., 2004; Stankowich and Coss, 2007). Explanations about differential persistence of traits under relaxed selection emphasize the cost of maintaining traits that are no longer useful and the possibility that more than one type of predators select for antipredator responses (Coss, 1999; Blumstein and Daniel, 2005). Indeed, a costly antipredator response is likely to disappear when the trait is no longer beneficial under relaxed selection. Moreover, the presence of a single predator may select for the persistence of antipredator responses even when many threats have disappeared (Blumstein, 2006).

Recent work with Père David's deer indicates that despite isolation from their predators over more than a thousand years, individuals have retained memories of

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sights and sounds associated with their former predators such as tigers (Li et al., 2011). Responding to the sight and sound of a predator is but one dimension of antipredator responses. Prey animals also show antipredator responses when predators are not seen or heard. For instance, individuals allocate time to scanning the habitat to detect potential threats (Caro, 2005). Individuals can allocate much time to vigilance often at the expense of other fitness-enhancing activities such as feeding although vigilance may be relatively cost-free in some species (Baker et al., 2011).

Antipredator vigilance is typically higher when predation risk is higher (Lima and Dill, 1990) and in gregarious species vigilance also varies as a function of group size (Elgar, 1989). In particular, individual investment in vigilance usually decreases with group size as more eyes and ears are available to scan the habitat (Pulliam, 1973). In addition, predation risk can be diluted among more individuals should an attack occur (Bertram, 1978). Interestingly, this group-size effect on vigilance often disappears in species that experience relaxed predation (Catterall et al., 1992; Blumstein et al., 2004) although this is not always the case (Blumstein et al., 2001; Shi et al., 2010). These findings can be of practical importance in a reintroduction programme where individuals would benefit from keeping vigilance at low, constant levels, allowing them to allocate more time to feeding, and thus adjust more easily to new foraging contingencies.

We examined the effect of group size on vigilance in a semi-free ranging population of Père David's deer reintroduced nearly 25 years ago in China. In the summer, deer graze on naturally occurring grasses but get food supplements in winter. No actual predation threats are present in the reserve. Deer forage in single- and mixed-sex groups that occupy two distinct zones except in winter where deer gather in large mixed-sex groups at sites with supplemental food. These two zones differ in the level of disturbance caused by people. The presence of people is often perceived as a threat (Frid and Dill, 2002), and animals in many species often invest more time on vigilance when disturbance levels are higher (e.g. Burger and Gochfeld, 1991; Jayakody et al., 2008; Wang et al., 2011). Archaeological evidence also suggests that deer were hunted in China for thousands of years (Cao et al., 1990). In the reserve, Père Davis's deer reacted to human disturbance by showing more alert responses such as staring (Li et al., 2007).

If human disturbance is perceived as predation risk, we predicted that vigilance levels would be higher in the more disturbed zone and that vigilance should decrease with group size even though threats from predators have been non-existent for an extended period of time. We examined such trends in male and female groups and also in mixed-sex groups. In a polygynous species such as Père David's deer, males compete with one another and also harass females. Therefore, vigilance may be aimed not only at threats occurring outside the group but also at threats caused by male behavior. Such vigilance related to intra- and inter-sexual competition has been documented in several species. For instance, territorial male impala *Aepyceros melampus* and giraffe *Giraffa camelopardalis* allocated more time to vigilance against intruding rivals (Shorrocks and Cocayne, 2005; Cameron and Du Toit, 2005). Female giraffe were the most vigilant when a potentially threatening male was nearby (Cameron and Du Toit, 2005). Sexual differences in the effect of group size on vigilance are thus expected given that the targets of vigilance may vary between the sexes (see Beauchamp 2008 for a recent review). In particular, the expected decrease in vigilance with group size may be dampened in groups with males if vigilance is also aimed at threats that occur within the group since such threats may become more prominent in larger groups (Beauchamp, 2001; Favreau et al., 2010; Li et al., 2012). Finally, the effect of relaxed predation pressure may vary between the sexes if the targets of vigilance are different for each sex and would be strongest for the sex that faces fewer threats from inside the group. Sexual differences in the response to relaxed predation pressure have been noted in one species (Lung and Childress, 2007) but not in another (Shi et al., 2010), suggesting that predation risk is not potentially the only factor influencing vigilance patterns.

1 Materials and Methods

1.1 Study site and study subjects

This study was conducted in the Dafeng Père David's deer National Nature Reserve (32°59′–33°03′N, 120°47′–120°53′E) in Jiangsu Province, China. The reserve is located on the Yellow Sea coast in eastern China and lies 2–4 m above sea level. Annual average temperature is 14.1℃, with an average temperature of 0.8℃ in January, 27.0℃ in July and 217 frost-free days. Average precipitation is 1068 mm with rain falling mostly between June and September. Local vegetation is dominated by cogongrass *Imperata cylindrica*, reed *Phragmites australis*, locust false-indigo *Amopha fruticosa* and locust *Robinia pseudoacacia*. Dafeng Nature Reserve consists of three core zones, two of which are enclosed by fences

allowing Père David's deer to range freely. Our study was conducted in the two fenced core areas. Visitors are allowed in one core area but not in the other thus creating two zones with different levels of human disturbance (high versus low).

Père David's deer is an endangered species. A herd of 39 Père David's deer was reintroduced in the reserve in 1986. After 25 years of conservation and development, the population as of 2011 numbers 1789 making it the world's largest population kept in semi-natural enclosures. In addition, the reserve started a rewilding programme in 1998 and the wild population has grown to 182 deer in 2011.

1.2 Behavioral sampling

The study was conducted during the rutting season (June to August) in 2010 and 2011. We walked along trails in each core zone every day looking for deer groups. A group was defined as a collection of individuals with no more than 50 m separating any two deer. Solitary hinds, which could be herded by males, were also included in the group. We videotaped groups of deer using a digital camcorder. Selection of focal individuals for behavioral sampling was done when viewing the tapes later. Groups of deer were often large and to obtain sufficiently detailed information for eventual focal subjects, we aimed the camera at one part of the group before moving on to another part after a set period of 20 min. Observations for a given group ended when group size changed or after two hours, whichever came first. While the animals were not marked, it was unlikely that the same individuals were sampled more than once on a given day given the large size of the groups. To minimize observer effects, we made observations at least 150 m away from any group (Li et al., 2007).

During the video analysis stage, we randomly selected at most four individuals of the same group for focal observations. For each individual, we noted in which zone observation took place, sex, group size and group type (all-male and all-female group, or mixed-sex group). Focal observations lasting less than 10 min were discarded. We noted the time allocated to vigilance during each focal observation. Vigilance occurred when a deer raised its head above the horizontal plane to scan the surroundings. From the videotapes, we calculated the percentage of time spent allocated to vigilance during each focal observation.

1.3 Statistical analysis

The dataset consisted of 324 focal observations collected from 153 groups over two years. Most individuals were sampled in groups that contained male and female deer (n = 262; 81%) but focal observations also took place in all-female groups (n = 36; 11%) and in all-male groups (n = 26; 8%). Overall, median group size was 17 and groups included from 1 to 303 individuals. Focal observations lasted on average 19.5±0.2 min. Time spent vigilant was 3.8% on average and ranged from 0 to 52.3%.

Percentage time spent vigilant was arcsine square-root transformed while group size was $\log_{10}$ transformed to meet requirements for the linear models. Focal observations where deer did not feed were not included so as to focus on actively feeding groups. We first analyzed time spent vigilant in single-sex groups using a mixed linear model including year and group id nested within the year as independent random factors, the latter to take into account multiple focal observations within the same groups. Fixed independent factors included sex, zone, and group size treated as a continuous factor. We also considered two-way interactions between independent variables. Non-significant interactions were not retained in the final model. Second, we analyzed time spent vigilant in mixed-sex groups using a similar mixed linear model. Finally, we compared vigilance in single- and mixed-sex groups for male and female subjects separately using group type as a fixed independent factor. Back-transformed means and confidence intervals are shown below.

2 Results

In single-sex groups, mean time spent vigilant was higher in females (7.3%, 0–35.0) than in males (2.2%, 0–23.6), controlling for zone and group size ($F_{1,27}$ = 15.9, $P < 0.001$; Fig. 1). Mean time spent vigilant was also higher in the more disturbed zone (9.8%, 0–39.6) than in the less disturbed one (1.1%, 0–20.0), controlling for sex and group size ($F_{1,27}$ = 16.0, $P < 0.001$). In addition, there was a significant interaction between sex and group size ($F_{1,27}$ = 6.4, P = 0.02) and between sex and level of disturbance ($F_{1,27}$ = 16.2, $P < 0.001$) on individual time spent vigilant. Mean time spent vigilant decreased significantly with group size in female groups (β [SE] = -0.14 [0.067], t = -2.1, P = 0.04) but not in male groups (β [SE] = 0.067 [0.048], t = 1.4, P = 0.17; Fig. 1). Mean time spent vigilant in male groups was significantly higher in the more disturbed zone (10.9%, 0–41.5) than in the less disturbed one (0%, 0–10.7; t = 4.5, $P < 0.001$). In female groups, mean time spent vigilant in the more disturbed zone (8.7%, 0–38.0) increased when compared to the less disturbed zone (6.0%, 0–32.5), but this effect was not statistically significant (t = 1.2, P = 0.24).

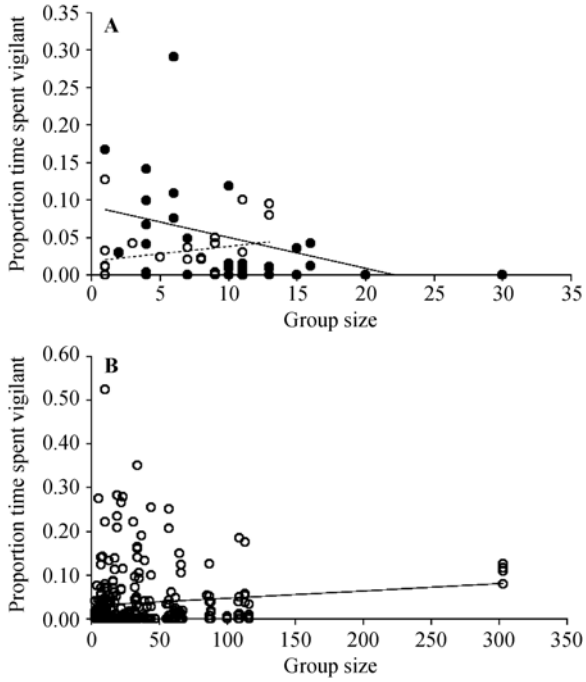

Fig. 1 Proportion of time spent vigilant by focal individuals in groups of Père David's deer as a function of group size in single-sex groups (A) (closed dots for females and open dots for males) and mixed-sex groups (B) (all sexes combined)

Trend lines are shown for each type of group.

In mixed-sex groups, mean time spent vigilant in females (2.0%, 1.1–3.2]) did not differ statistically from that in males (2.4%,1.3–3.7; $F_{1,158}$ = 0.45, P = 0.22). Mean time spent vigilant did not vary with group size (β [*SE*] = 0.034 [0.028]; $F_{1,158}$ = 1.4, P = 0.23; Fig. 2) or level of disturbance ($F_{1,158}$ = 1.5, P = 0.22).

In the two types of groups including females, mean time spent vigilant by females was smaller in single-sex (0.57%, 0–3.1)) than in mixed-sex groups (1.8%, 0.45–3.9; $F_{1,102}$ = 11.3, P < 0.001), controlling for zone and group size. In the two types of groups including males, mean time spent vigilant by males in single-sex groups (2.3%, 0.59–5.1) did not differ statistically from that in mixed-sex groups (2.3%, 0.25–6.3; $F_{1,46}$ = 0.0, P = 0.99), again controlling for zone and group size.

3 Discussion

The results of our study showed sexual differences in group-size effect and reaction to various human-disturbance levels. Given the lack of direct contact with predators, the effect of group size and human disturbance levels on vigilance that we documented here certainly suggest that Père David's deer consider human presence as a threat, as has been documented in other mammalian species (e.g. Papouchis et al., 2001; Manor and Saltz, 2003; Jayakody et al., 2008).

Considering single-sex groups first, we found that group size interacted significantly with sex. In particular, time spent vigilant decreased significantly with group size but only in female groups. The group-size effect on vigilance has been documented in several mammalian species facing predation threats (see Li et al., 2008; Li et al., 2009; Michelena and Deneubourg, 2011; Pays et al., 2012 for recent examples). It is perhaps the case that human pressure, as described above, helped maintain antipredator responses in Père David's deer despite the loss of contact over time with natural enemies. Indeed, it was hypothesized that the presence of a single type of threat may be sufficient to maintain antipredator responses in the face of relaxed predation pressure (Blumstein, 2006).

To account for the lack of effect of group size on vigilance in all-male groups, we need to invoke another kind of disturbance, which occurs within rather than outside groups. In rutting season, males compete with one another for mating opportunities (Jiang et al., 2004). Indeed, we have witnessed much fighting in all-male groups. In rutting season, adult male elk *Cervus elaphus* showed a significant increase in aggression from 1% to 7% of their time active (Lung and Childress, 2007). Such disturbance within a group is likely to increase with group size, and vigilance directed at companions in the group is thus expected to increase with group size, counteracting the negative effect of group size on vigilance aimed at outside threats. Positive frequency-dependent factors, such as aggression, have been shown to dampen the negative effect of group size on vigilance (Slotow and Coumi, 2000; Beauchamp, 2001; Favreau et al., 2010).

In mixed-sex groups, the negative effect of group size on vigilance disappeared in females. In rutting season, male deer often harass females for mating opportunities. For instance, males sniff females, chase them, and try to mate with them. Vigilance in females may thus be partly aimed at detecting harassing males. A social component to vigilance behavior has been suggested in several species (e.g. Treves, 1999; Hirsch, 2002; Li et al. 2012). This argument would explain why vigilance failed to decrease with group size in larger mixed-groups, where the potential for harassment is higher, and why females in mixed-sex groups invested more time in vigilance than in single-sex groups, controlling for group size.

We now turn to the effect of disturbance levels caused by human activity. Vigilance increased with dis-

turbance levels in general but this effect was stronger in male-only than in female-only groups. Higher vigilance in more disturbed areas has been documented in many species (e.g. Manor and Saltz, 2003; Jayakody et al., 2008; Wang et al., 2011). Beyond the issue of statistical power, we note that our classification of threat levels caused by human activity is quite coarse, and it is possible that females differed from males in terms of exposure to human activity even within the same core zones. Another possibility is that females, which are already more vigilant than males (7.3% for females versus 2.2% for males), are more limited in the extent to which vigilance may be increased in more disturbed areas. A ceiling effect was suggested by Manor et al. (2003) to explain lack of responses to human disturbance in mammals.

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References

Baker DJ, Stillman RA, Smart SL, Bullock JM, Norris KJ, 2011. Are the costs of routine vigilance avoided by granivorous foragers? Funct. Ecol. 25(3): 617–627.

Beauchamp G, 2001. Should vigilance always decrease with group size? Behav. Ecol. Sociobiol. 51: 47–52.

Berger J, Swenson JE, Persson IL, 2001. Recolonizing carnivores and naive prey: Conservation lessons from Pleistocene extinctions. Science. 291: 1036–1039.

Bertram CR, 1978. Living in groups: predator and prey. In: Krebs JR, Davies NB ed. Behavioral Ecology. Oxford: Blackwell, 64–96.

Blumstein DT, 2006. The multipredator hypothesis and the evolutionary persistence of antipredator behavior. Ethology 112: 209–217.

Blumstein DT, Daniel JC, 2002. Isolation from mammalian predators differentially affects two congeners. Behav. Ecol. 13: 657–663.

Blumstein DT, Daniel JC, 2005. The loss of anti-predator behavior following isolation on islands. Proc. R. Soc. B. 272: 1663–1668.

Blumstein DT, Daniel JC, McLean IG, 2001. Group size effects in quokkas. Aust. J. Zool. 49: 641–649.

Blumstein DT, Daniel JC, Springett BP, 2004. A test of the multi-predator hypothesis: Rapid loss of antipredator behavior after 130 years of isolation. Ethology. 110: 919–934.

Burger J, Gochfeld M, 1988. Effects of group size and sex on vigilance in ostriches *Struthio camelus*: Antipredator strategy or mate competition? Ostrich. 59: 14–20.

Byers JA, 1997. American Pronghorn: Social Adaptations and the Ghosts of Predation Past. Chicago: Univ. of Chicago Press.

Cameron EZ, Du Toit JT, 2005. Social influences on vigilance behaviour in giraffes *Giraffa camelopardalis*. Anim. Behav. 69: 1337–1344.

Cao K, Qiu L, Chen B, Miao M, 1990. Chinese Milu. Shanghai: Xuelin Press.

Caro TM, 2005. Antipredator defenses in birds and mammals. Chicago: Univ. of Chicago Press.

Catterall CP, Elgar MA, Kikkawa J, 1992. Vigilance does not covary with group size in an island population of silvereyes *Zosterops lateralis*. Behav. Ecol. 3: 207–210.

Coss RG, 1999. Effects of relaxed natural selection on the evolution of behavior. In: Foster SA, Endler JA ed. Geographic Variation in Behavior: Perspectives on Evolutionary Mechanisms. Oxford: Oxford Univ. Press, 180–208.

Elgar MA, 1989. Predator vigilance and group size in mammals and birds. Biol. Rev. 64: 13–33.

Favreau FR, Goldizen AW, Pays O, 2010. Interactions among social monitoring, anti-predator vigilance and group size in eastern grey kangaroos. Proc. R. Soc. B. 277: 2089–2095.

Frid A, Dill LM, 2002. Human-caused disturbance stimuli as a form of predation risk. Conserv. Ecol. 6: 11.

Griffin AS, Blumstein DT, Evans CS, 2000. Training captive-bred or translocated animals to avoid predators. Conserv. Biol. 14: 1317–1326.

Hirsch BT, 2002. Social monitoring and vigilance behavior in brown capuchin monkeys *Cebus apella*. Behav. Ecol. Sociobiol. 52: 458–464.

Jayakody S, Sibbald AM, Gordon IJ, Lambin X, 2008. Red deer *Cervus elephus* vigilance behavior differs with habitat and type of human disturbance. Wildlife Biol. 14: 81–91.

Jiang Z, Feng Z, Yu C, Zhang L, Xia J et al., 2000. Reintroduction and recovery of Père David's deer in China. Wildlife. Soc. Bull. 28: 681–687.

Jiang Z, Li C, Zeng Y, 2004. "Harem defending" or "challenging": Alternative individual mating tactics in Pere David's deer under different time constraint. Acta Zool. Sin. 50: 706–713.

Lahti DC, Johnson NA, Ajie BC, Otto SP, Hendry AP et al., 2009. Relaxed selection in the wild. Trends. Ecol. Evol. 24: 487–496.

Li C, Jiang Z, Li L, Li Z, Fang H et al., 2012. Effects of reproductive status, social rank, sex and group size on vigilance patterns in Przewalski's gazelle. Plos one. 7: 32607.

Li C, Jiang Z, Tang S, Zeng Y, 2007. Evidence of effects of human disturbance on alert responses in Père David's deer *Elaphurus davidianus*. Zoo. Biol. 26: 461–470.

Li C, Yang X, Ding Y, Zhang L, Fang H et al., 2011. Do Père David's deer lose memories of their ancestral predators? Plos One. 6: e23623.

Li Z, Jiang Z, 2008. Group size effect on vigilance: Evidence from Tibetan gazelle in Upper Buha River, Qinghai-Tibet Plateau. Behav. Process. 78: 25–28.

Li Z, Jiang Z, Beauchamp G, 2009. Vigilance in Przewalski's gazelle: Effects of sex, predation risk and group size. J. Zool. 277: 302–308.

Lima SL, Dill LM, 1990. Behavioral decisions made under the risk of predation: a review and prospectus. Can. J. Zool. 68: 619–640.

Lung MA, Childress MJ, 2007. The influence of conspecifics and predation risk on the vigilance of elk *Cervus elaphus* in Yellowstone National Park. Behav Ecol. 18(1): 12–20.

Manor R, Saltz D, 2003. Impact of human nuisance disturbance on vigilance and group size of a social ungulate. Ecol. Appl. 13: 1830–1834.

Michelena P, Deneubourg JL, 2011. How group size affects vigilance dynamics and time allocation patterns: The key role of imitation and tempo. Plos One. 6: e18631.

Papouchis CM, Singer FJ, Sloan WB, 2001. Responses of desert bighorn sheep to increased human recreation. J. Wildlife. Manage. 65: 573–582.

Pays O. Sirot E, Fritz H, 2012. Collective vigilance in the Greater Kudu: Towards a better understanding of synchronization patterns. Ethology. 118: 1–9.

Placyk JS, Burghardt G, 2011. Evolutionary persistence of chemicallyelicited ophiophagous antipredator responses in gartersnakes *Thamnophis sirtalis*. J. Comp. Psychol. 125: 134–142.

Pulliam HR, 1973. On the advantages of flocking. J. Theor. Biol. 38: 419–422.

Shi JB, Beauchamp G, Dunbar RIM, 2010. Group-size effect on vigilance and foraging in a predator-free population of feral goats *Capra hircus* on the Isle of Rum, NW Scotland. Ethology 116: 329–337.

Shorrocks B, Cockayne A, 2005. Vigilance and group size in impala *Aepyceros melampus*: A study in Nairobi National Park, Kenya. Afr. J. Ecol. 43: 91–96.

Slotow R, Coumi N, 2000. Vigilance in bronze mannikin groups: The contributions of predation risk and intra-group competition. Behavior. 137: 565–578.

Stankowich T, Coss R, 2007. The re-emergence of felid camouflage with the decay of predator recognition in deer under relaxed selection. Proc. R. Soc. B. 274: 175–182.

Treves A, 1999. Within-group vigilance in red colobus and redtail monkeys. Am. J. Primatol. 48: 113–126.

Wang Z, Li Z, Beauchamp G, Jiang Z, 2011. Flock size and human disturbance affect vigilance of endangered red-crowned cranes *Grus japonensis*. Biol. Conserv. 144: 101–105.