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Behavioural habituation undermines deterrents in rhesus macaque crop raiding in Eastern Ghats, India

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Abstract

Human–wildlife conflict caused by crop-raiding primates represents a major conservation and livelihood challenge in human-modified landscapes, yet the long-term effectiveness of mitigation strategies remains poorly understood because behavioural habituation may reduce deterrent efficacy over time. We evaluated the influence of habitat context and behavioural habituation on the performance of five crop protection strategies against crop-raiding rhesus macaques (*Macaca mulatta*) over three consecutive cropping seasons (2023–2025) in the Eastern Ghats, India. Field experiments were conducted across two contrasting habitat types—forest fringe and forest fringe associated with human settlements—and compared low-cost solar fencing, nylon netting, bear scare devices, agri cannons and conventional manual watching. Crop damage, macaque visitation, troop characteristics and comparative economic performance were assessed using generalized linear models and correlation analyses. Crop damage differed significantly among treatments, habitats and seasons, with deterrent-based methods showing progressive declines in effectiveness across seasons, consistent with behavioural habituation. In contrast, low-cost solar fencing provided consistently effective protection throughout the study. Forest fringe sites associated with human settlements supported larger, more frequently encountered macaque troops and experienced greater crop damage than forest-edge sites. Crop damage was strongly associated with macaque visitation in both habitat types, while comparative economic performance mirrored ecological effectiveness, with solar fencing providing the most favourable returns under commercial farming conditions. Our findings demonstrate that behavioural habituation is a key determinant of the long-term success of wildlife conflict mitigation and highlight the importance of management strategies based on sustained physical exclusion rather than novelty-dependent deterrents. These results provide practical guidance for improving non-lethal management of crop-raiding primates in rapidly changing agricultural landscapes.

Introduction

Human–wildlife conflict from crop raiding is a major conservation and socioeconomic challenge where agriculture borders natural habitats (Distefano 2005; Treves and Karanth 2003; Nyhus 2016; Anand et al. 2018). Agricultural expansion, habitat fragmentation and increased human–wildlife overlap have intensified interactions at forest–agriculture boundaries, producing substantial economic losses and complicating management (Carter et al. 2012; Koirala et al. 2021). Although a range of non-lethal mitigation strategies exists, their long-term success depends on animal behaviour: behaviourally flexible species may rapidly habituate to deterrents, reducing effectiveness over time (Feuerbacher et al. 2021). Despite growing recognition of behavioural adaptation, few studies quantify how mitigation performance changes across multiple seasons and contrasting ecological settings.

Primates are particularly challenging crop raiders because of high cognitive ability, behavioural plasticity and ease of exploiting anthropogenic foods (McLennan and Hockings 2014; Hockings et al. 2015). The rhesus macaque (Macaca mulatta) is widespread in South Asia and a major source of crop damage in India; large troop sizes, rapid learning and reduced fear of humans facilitate repeated exploitation of

profitable crops (Pirta et al. 1997; Chauhan and Sharma 2004; Kannan et al. 2010; Saraswat et al. 2015; Rathi and Bhatt 2020). Habitat context influences both raiding intensity and mitigation durability: populations near settlements often form larger, more human-acclimated troops with lower neophobia, which may accelerate habituation to deterrents (Saraswat et al. 2015; Hockings et al. 2015). Empirical evidence linking habitat context to seasonal changes in mitigation effectiveness remains limited.

In the Eastern Ghats of Andhra Pradesh, rice-based agroecosystems abut forest margins, creating persistent farmer–wildlife interfaces where land-use change, crop attractiveness and behavioural adaptation drive substantial economic losses (Pragadeesh et al. 2025; Namala et al. 2026). We present a three-year field study that examines how behavioural habituation and habitat context affect the effectiveness of five commonly used non-lethal crop protection strategies against *M. mulatta*. We hypothesised that deterrent-based interventions would decline in effectiveness via habituation, while physical exclusion would provide more consistent protection. Our objectives were to (i) quantify habitat-related differences in raiding intensity and troop characteristics, (ii) evaluate temporal changes in mitigation effectiveness over three cropping seasons, and (iii) compare the relative economic performance of these strategies for smallholders. By integrating behavioural, ecological and economic perspectives, the study aims to inform more durable non-lethal approaches to mitigating human–primate conflict.

Material and methods

Study area and habitat classification

The study was conducted during three consecutive Kharif seasons (2023–2025) across 12 villages in the Eastern Ghats forest-fringe zone of Andhra Pradesh, India. Two habitat types were defined based on landscape structure and degree of human presence. Forest fringe (FF) sites (n = 6) comprised Konalova, Nagulagudem and Buttayagudem (West Godavari District), and Singampalli, Sunnampadu and Musurumilli (East Godavari District). These sites included rice fields adjoining continuous forest with minimal human settlement. Forest fringe with human population (FFHP) sites (n = 6) comprised Rampa, Rampachodavaram and Maredumilli (East Godavari District), and Kamavarapukota, Dwaraka Tirumala and V.R. Gudem (West Godavari District). These sites consisted of rice fields interspersed with human settlements near forest margins, where supplementary food and frequent human contact promote sustained macaque presence. Each village was treated as an independent experimental replicate (n = 6 per habitat).

Selection of experimental sites and fields

Villages with recurrent rhesus macaque, *M. mulatta* damage were identified through preliminary surveys (Namala et al. 2026). Within each selected village, five comparable irrigated transplanted rice fields (~ 2 ha each) were chosen based on farmer willingness, accessibility, similar field size, crop growth stage

and rice variety. Fields were intended to represent typical smallholder conditions and were not selected on the basis of observed damage intensity. Each village therefore provided five fields that served as experimental units within the location.

Experimental design

We used a habitat × season × treatment factorial design. Seasons were S1 (2023), S2 (2024) and S3 (2025). Five crop protection strategies were evaluated: solar fencing (T1), nylon netting (T2), bear scare device (T3), agri cannon (T4) and manual watching (T5, the prevailing farmer practice). Within each village, the five fields were randomly assigned to one of the five treatments. To avoid pseudoreplication, field-level measurements were averaged to produce a single location-level observation per treatment per season, yielding 180 location-level observations (6 locations × 2 habitats × 5 treatments × 3 seasons). Standard agronomic practices recommended by ANGRAU were followed uniformly across treatments. All procedures complied with CPCSEA guidelines and were approved by the Institutional Animal Ethics Committee, ANGRAU (IAEC/VPM/2021-22, dated 15 March 2022).

Crop protection strategies

Solar fencing (T1): Low-cost solar-powered fence using bamboo/wooden poles (2.1–2.4 m) supporting 16-gauge galvanised iron wires energised by a 12 V rechargeable battery. Wire spacing: lowest strand at 0.15 m, subsequent strands at 0.3–0.45 m. Vegetation was cleared fortnightly to prevent earthing; fence integrity was maintained. The pulsating current provided a mild, non-lethal aversive stimulus.

Nylon netting (T2)

High-density nylon netting (1.8–2.1 m height) installed around fields as a physical barrier; integrity monitored regularly.

Bear scare device (T3): Costumed human deterrent deployed during peak macaque activity (06:00–07:00 h and 16:30–18:00 h).

Agri cannon (T4)

Calcium carbide-based acoustic device producing explosive sounds via acetylene ignition, operated manually at field boundaries during peak activity.

Manual watching (T5)

Conventional farmer practice and active reference treatment. One trained hired labourers per ~2-ha field deterred macaques by shouting, throwing small stones and using trained dogs during peak activity. The same personnel and protocol were used across seasons and locations.

Note

An untreated control (no protection) was not included because farmers declined to leave commercial rice fields unprotected under conditions of severe, recurrent macaque raiding. The experiment therefore compares alternative strategies against the prevailing farmer practice rather than against absence of management.

Crop damage assessment and macaque visitation

Crop damage was assessed at four growth stages (vegetative, maximum tillering, heading, milky grain) using 10 randomly placed 1 m2 quadrats per field per stage. Damaged tillers were identified by characteristic macaque feeding signs: panicle removal, bite marks, grain scatter, scats and tracks. Damage proportion was calculated as damaged tillers / total tillers per quadrat and averaged to field and then location level.

Macaque visitation was recorded using standardised 30-minute observation sessions at dawn and dusk. A visitation event was defined as a troop entry separated by ≥ 30 minutes from the preceding entry. Troop size was estimated by direct counts during each visit.

Economic analysis

Economic performance was evaluated using the cost:benefit (C:B) ratio per hectare per season: C:B ratio = gross return / total cost. Gross return was estimated from total yield value per hectare using the Minimum Support Price (MSP) for paddy fixed at Rs 2260 per quintal for all seasons. Total cost included materials, installation (amortised over service life) and labour, recorded at each location.

Statistical analysis

All inferential analyses used location-level observations (one observation per village × treatment × season); field-level measurements were averaged to avoid pseudoreplication. The primary response variable was proportion crop damage per treatment per village per season. Proportions were analysed with a quasibinomial generalized linear model (GLM) with logit link to account for overdispersion (Crawley 2012), preferred to arcsine transformation (Warton and Hui 2011). Fixed effects were treatment (5 levels), habitat (2 levels), season (3 levels) and their interactions. Model significance was assessed with quasi-F tests.

Macaque visitation counts were analysed using a negative binomial GLM with log link to account for overdispersion; effect sizes are presented as incidence rate ratios (IRR = exp(coefficient)). Associations between macaque visitation and crop damage, and between protection efficiency and yield, were tested using Spearman's rank correlation (r_s). Analyses were performed in R v4.3.1 (R Core Team 2023). Statistical significance was set at $P < 0.05$.

Results

Effects of habitat, season and treatment on crop damage

A quasibinomial GLM showed that crop damage was influenced by treatment, habitat and season (Table 1). Treatment had the largest effect ($F(4,175) = 762.52$, $p < 0.001$), followed by habitat ($F(1,174) = 196.45$, $p < 0.001$) and season ($F(2,172) = 43.52$, $p < 0.001$). Crop damage increased across seasons in both habitats (Fig. 1). A significant treatment × habitat interaction ($F(4,168) = 6.02$, $p < 0.001$) indicated treatment effectiveness differed between habitats, and a treatment × season interaction ($F(8,160) = 2.64$, $p = 0.010$) indicated temporal variation in performance (Fig. 1). Habitat × season ($p = 0.799$) and the three-way interaction ($p = 0.718$) were not significant.

Table 1
Quasibinomial GLM results for crop damage proportions in rice across habitat, season, and treatment, Eastern Ghats forest fringe landscapes of Andhra Pradesh (Kharif 2023–2025).

Term	df	F value	p-value
Treatment	4, 175	762.52	< 0.001
Habitat	1, 174	196.45	< 0.001
Season	2, 172	43.52	< 0.001
Treatment × Habitat	4, 168	6.02	< 0.001
Treatment × Season	8, 160	2.64	0.01
Habitat × Season	2, 158	0.23	0.799 ns
Treatment × Habitat × Season	8, 150	0.67	0.718 ns
ns, not significant			

Crop damage and macaque visitation

Solar fencing (T1) consistently recorded the lowest damage across habitats and seasons (Fig. 1). Deterrent treatments (T3, T4, T5) showed increasing damage from S1 to S3, whereas physical exclusion methods (T1, T2) remained comparatively stable (Fig. 1). Macaque visitation differed among treatments ($\chi^2 = 23.53$, $df = 4$, $p < 0.001$) but not by habitat ($\chi^2 = 0.72$, $df = 1$, $p = 0.397$) or season ($\chi^2 = 2.65$, $df = 2$, $p = 0.265$); no interaction effects were detected (Fig. 2).

Relationship between visitation and damage

Macaque visitation was strongly positively correlated with crop damage in both habitats (FF: $rs = 0.75$; FFHP: $rs = 0.73$; $p < 0.001$; Fig. 3).

Protection efficiency, yield and economics

Solar fencing (T1) had the highest protection efficiency across habitats and seasons, followed by nylon netting (T2), bear scare (T3) and agri cannon (T4); manual watching (T5) performed worst (Fig. 4). Protection efficiency correlated positively with rice yield ($r_s = 0.81$, $p < 0.001$). Cost–benefit ratios were highest for solar fencing (FF: 1.7; FFHP: 1.5), followed by nylon netting and bear scare (1.4 in FF; 1.2 in FFHP), then agri cannon (1.3 in FF; 1.2 in FFHP). Manual watching returned 1.0 in FF and 0.9 in FFHP (Table 2).

Table 2
Cost-benefit (C:B) ratio of crop protection treatments across habitat types.

		(FF)		(FFHP)	
Treatment	**Total cost (Rs ha⁻¹)**	**Total yield (kg ha⁻¹)**	**C:B**	**Total yield (kg ha⁻¹)**	**C:B**
Solar Fencing (T1)	1,92,500	14,277	**1.7**	12,939	**1.5**
Nylon Netting (T2)	2,25,000	13,396	1.4	11,756	1.2
Bear Scare (T3)	2,13,000	13,305	1.4	11,497	1.2
Agri Cannon (T4)	2,10,500	12,075	1.3	10,701	1.2
Manual Watching (T5)	2,61,000	11,424	1.0	9,755	0.9

FF: forest fringe (n = 6 locations); FFHP: forest fringe with human population (n = 6 locations). Total cost = cultivation + protection investment (Rs ha⁻¹), pooled across three seasons (Kharif 2023–2025); costs were identical across habitats for each treatment. C:B = total return/total cost; paddy procurement price ₹2260 quintal⁻¹ applied uniformly. T5 = conventional farmer-practice baseline.

Rhesus macaque troop ecology across habitats

Troop characteristics differed between habitats: FFHP supported larger troops (79 ± 14 individuals) than FF (31 ± 8), with higher encounter frequency, greater female bias and a higher proportion of juveniles (Table 3). These patterns are consistent with previous reports (Saraswat et al. 2015; Pirta et al. 1997)

Table 3
Rhesus macaque (*Macaca mulatta*) troop characteristics at forest fringe (FF) and forest fringe with human population (FFHP) study sites.

Characteristic	(FF)	(FFHP)
Mean troop size	31 ± 8	79 ± 14
Range (troop size)	22–42	62–96
Sex ratio (M:F)	1:5.3	1:7.1
Mean group encounters per season	18 ± 4	47 ± 9
Proportion of juveniles (%)	22.4 ± 3.1	28.7 ± 4.2
Values are mean ± SD across all observation sessions per habitat.		

Discussion

Our three-season study demonstrates that the effectiveness of commonly used crop protection strategies against *Macaca mulatta* is strongly shaped by behavioural habituation and habitat context. Deterrent-based methods (acoustic, visual and human-based) declined in performance across seasons, whereas physical exclusion (solar fencing, nylon netting) remained comparatively stable (Fig. 1). The significant treatment × season interaction (Table 1) indicates that the observed declines reflect systematic temporal habituation rather than short-term variability.

Habituation to deterrents is well documented in crop-foraging primates (Hockings and McLennan 2012; McLennan and Hockings 2014), and our results corroborate this pattern. Acoustic devices exhibited the most rapid loss of effectiveness, likely because their predictable operation and conspicuous cues are readily learned and ignored with repeated exposure. Visual and human-based deterrents were initially effective but weakened over time. By contrast, solar fencing consistently produced the lowest crop damage (Fig. 1), supporting evidence that electric fencing provides reliable, non-lethal mitigation through consistent aversive reinforcement (Feuerbacher et al. 2021). Physical exclusion limits access irrespective of prior exposure and therefore reduces opportunities for behavioural adjustment (Hill 2018). Nylon netting, while acting as a passive barrier, showed slower decline and was occasionally breached through progressive structural probing, indicating that passive barriers can be undermined without sustained maintenance or reinforcement.

Habitat context modified both conflict intensity and mitigation performance. FFHP sites supported larger troops, higher encounter frequencies and a greater proportion of juveniles (Table 3), traits associated with increased foraging pressure and reduced neophobia (Saraswat et al. 2015; Pirta et al. 1997). These demographic and behavioural differences likely underpin the higher crop damage observed in FFHP and the significant treatment × habitat interaction (Table 1). Such patterns mirror reports from other human-

modified landscapes where frequent human contact and food subsidies promote behavioural flexibility and rapid adjustment to deterrents (Hockings et al. 2015; Riley 2013).

The strong positive correlation between macaque visitation and crop damage (FF: rs = 0.75; FFHP: rs = 0.73; Fig. 3) indicates that troop activity is a proximate driver of yield loss. That visitation did not vary significantly with habitat or season (Fig. 2) suggests that differences in damage across sites arise largely from variation in treatment effectiveness and troop composition rather than from visitation frequency per se. Comparable relationships have been documented in other primate–crop systems, where interaction between visitation intensity and behavioural responses determines net crop loss (Wallace and Hill 2012).

Economic outcomes reflected ecological effectiveness. Solar fencing yielded the highest cost–benefit ratios across habitats (Table 2), whereas manual watching—the prevailing smallholder practice—provided marginal or negative returns under high conflict. These results support the cost-effectiveness of physical barriers relative to labour-intensive deterrents in smallholder systems (Feuerbacher et al. 2021) and emphasise that mitigation strategies should be evaluated on both ecological and economic criteria.

Management implications and caveats

Our findings indicate that durable mitigation in macaque-affected agroecosystems will likely require measures that either physically exclude animals or combine exclusion with variable, unpredictable deterrents to reduce habituation. Solar fencing performed well where installed and maintained correctly; however, gaps, vegetation contact or poor maintenance reduced its effectiveness. Widespread adoption of exclusion may alter foraging patterns at larger spatial scales and could displace raiding to neighbouring unprotected fields or non-agricultural resources; landscape-level planning and community coordination are therefore essential (Osborn and Parker 2003).

Limitations and future directions

The absence of an untreated (no-protection) control constrains inference about absolute reductions in crop loss; treatments should be interpreted relative to manual watching, which served as the active reference under realistic farming conditions. The three-season duration captured consistent temporal trends but cannot fully characterise longer-term dynamics or multi-generational behavioural change. We did not explicitly model environmental covariates or individual troop histories, which may influence habituation trajectories. Future studies should extend monitoring over longer time frames, incorporate landscape-scale manipulations, and evaluate combined interventions (e.g., exclusion plus unpredictable deterrents) and social factors (community adoption, maintenance capacity) to identify scalable, durable solutions.

Conclusions

Behavioural habituation and habitat context determine how long non-lethal crop-protection methods remain effective against rhesus macaques. Over three Kharif seasons, deterrent methods (acoustic, visual and human-based) became less effective with repeated use. Acoustic devices lost effectiveness fastest. Physical exclusion, especially well-installed and maintained low-cost solar fencing, gave the most consistent protection and best economic returns. Sites near human settlements had larger, less fearful troops, higher damage and faster loss of deterrent efficacy. For smallholders, prioritise robust physical barriers, community coordination and regular maintenance. Where exclusion is not feasible, combine unpredictable or variable deterrents with landscape-level planning to reduce habituation and displacement. Future work should test long-term and landscape-scale effects of widespread exclusion and assess practical scalability under farmer conditions.

Declarations

Ethical approval

The study involved non-invasive field observations only. No animals were captured, handled, or restrained. The solar fencing system delivered a mild pulsating shock (12 V), which is non-injurious and does not constitute animal experimentation. The study was approved by the Institutional Animal Ethics Committee (IAEC), ANGRAU (Approval No. IAEC/VPM/2021-22, dated 15 March 2022) and conducted in accordance with national guidelines and the Wildlife Protection Act 1972.

Conflict of interest

The authors declare no conflict of interest.

Declarations of funding

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Author Contribution

SRN: Conceptualisation, methodology, investigation, data analysis, writing original draft. AKA, RBS: Field data collection and analysis. VKM: Data analysis and manuscript revision. SSA, PKK, NBN, VNC: Field selection, execution and farmer coordination. All authors approved the final manuscript.

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Data Availability

Data availability: The datasets generated and analysed during the current study are available from the corresponding author upon reasonable request.

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Figures

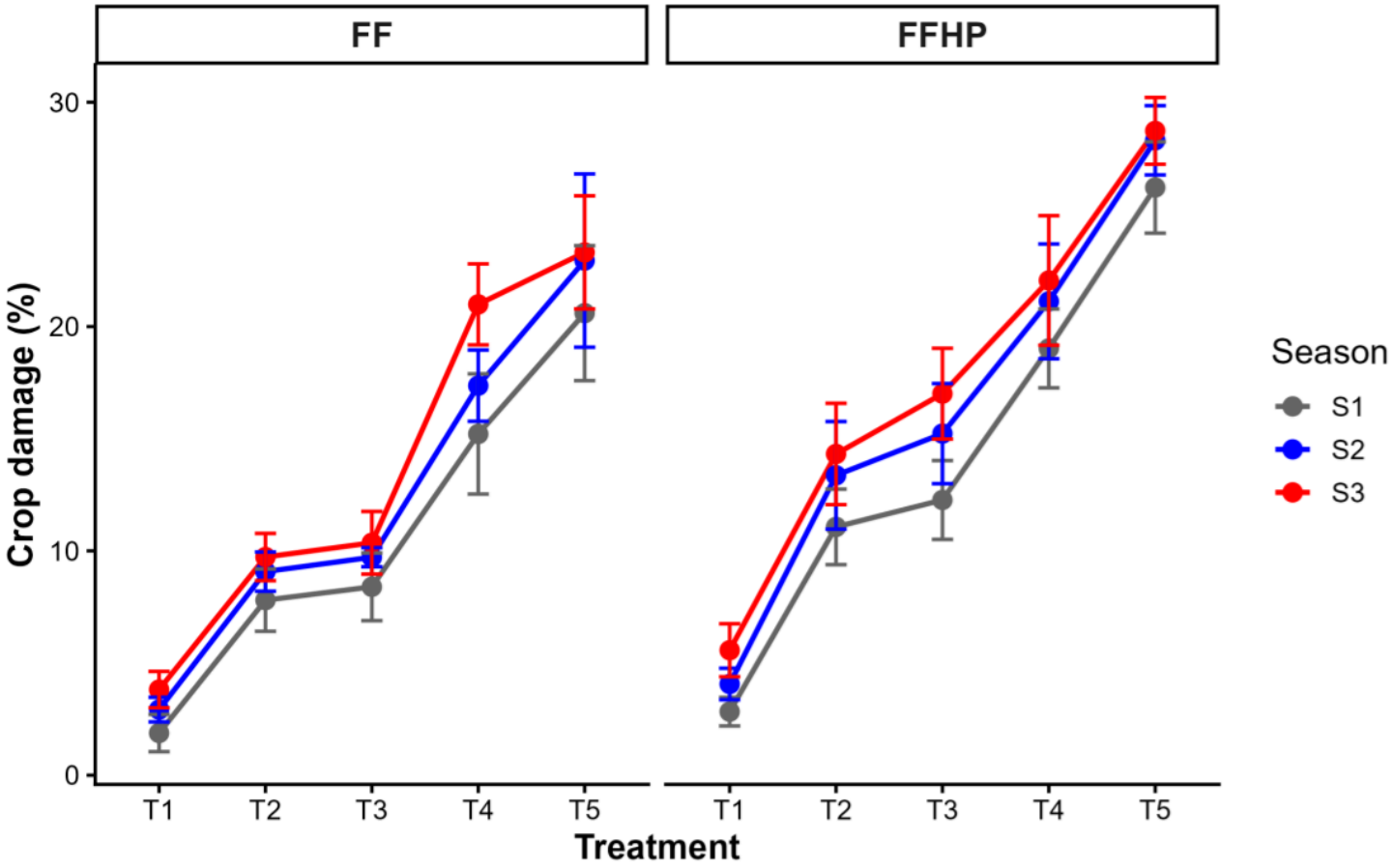


Figure 1

Effect of crop protection treatment and season on rhesus macaque-induced crop damage (%) in rice across forest fringe (FF) and forest fringe with human population (FFHP) habitats over three Kharif seasons (S1: 2023, S2: 2024, S3: 2025; n = 6 locations per habitat per season). Values are mean ± SD.

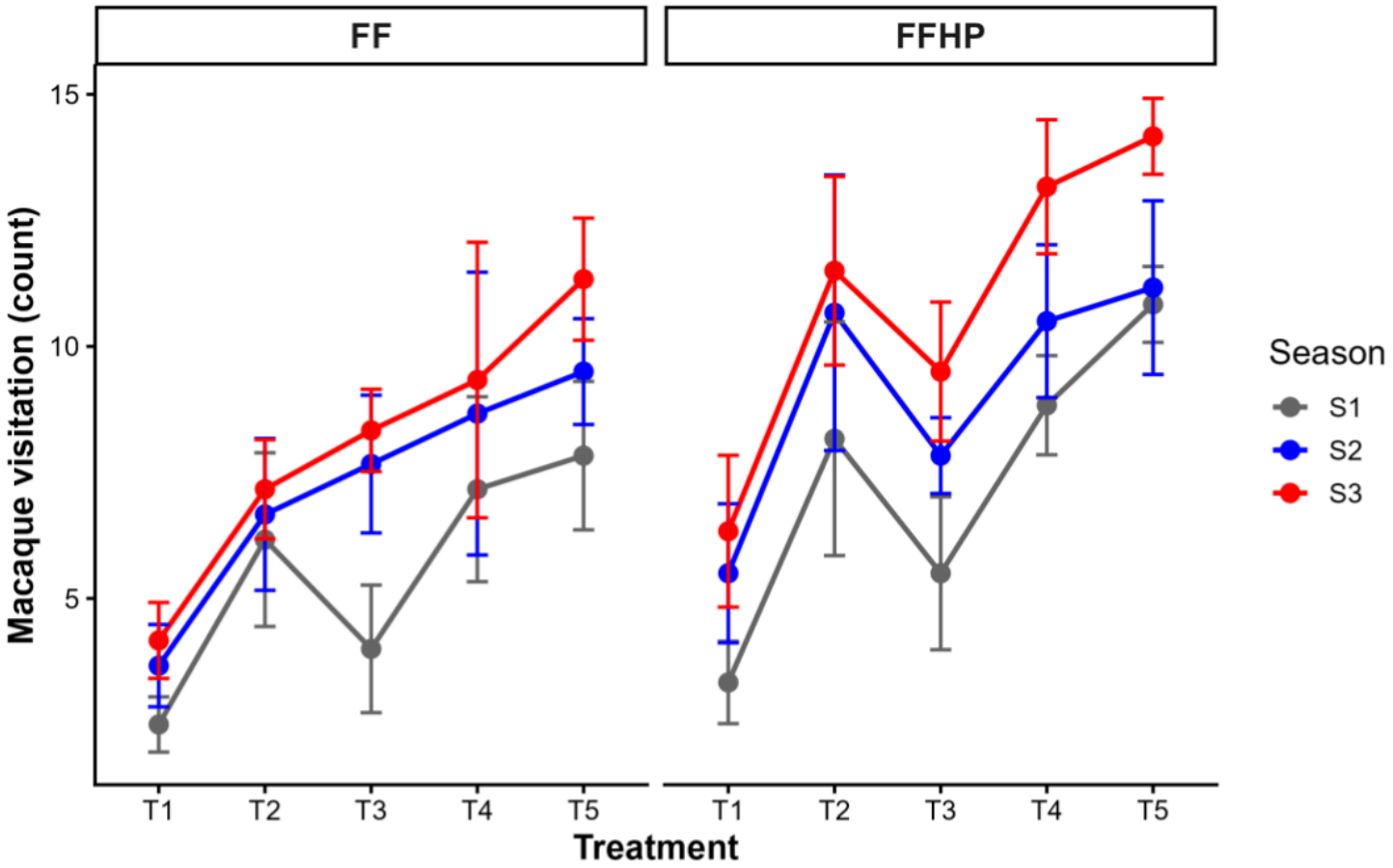


Figure 2

Effect of crop protection treatment and season on rhesus macaque (*Macaca mulatta*) visitation frequency in rice fields across forest fringe (FF) and forest fringe with human population (FFHP) habitats over three Kharif seasons (n = 6 locations per habitat per season). Values are mean ± SD.

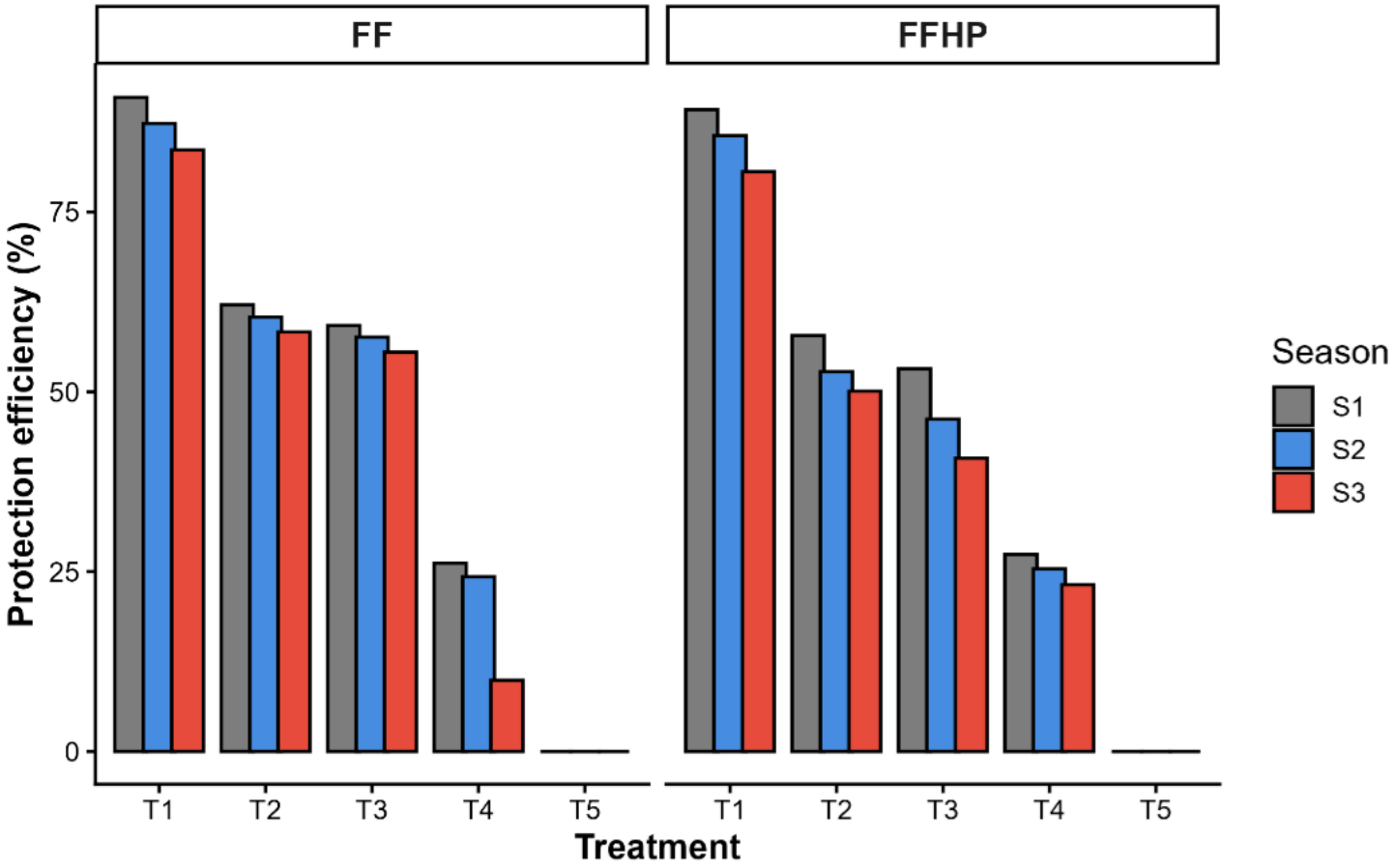


Figure 3

Protection efficiency (%) of crop protection treatments across habitat types and three Kharif seasons (S1: 2023, S2: 2024, S3: 2025; n = 6 locations per habitat per season). Calculated relative to T5 baseline.

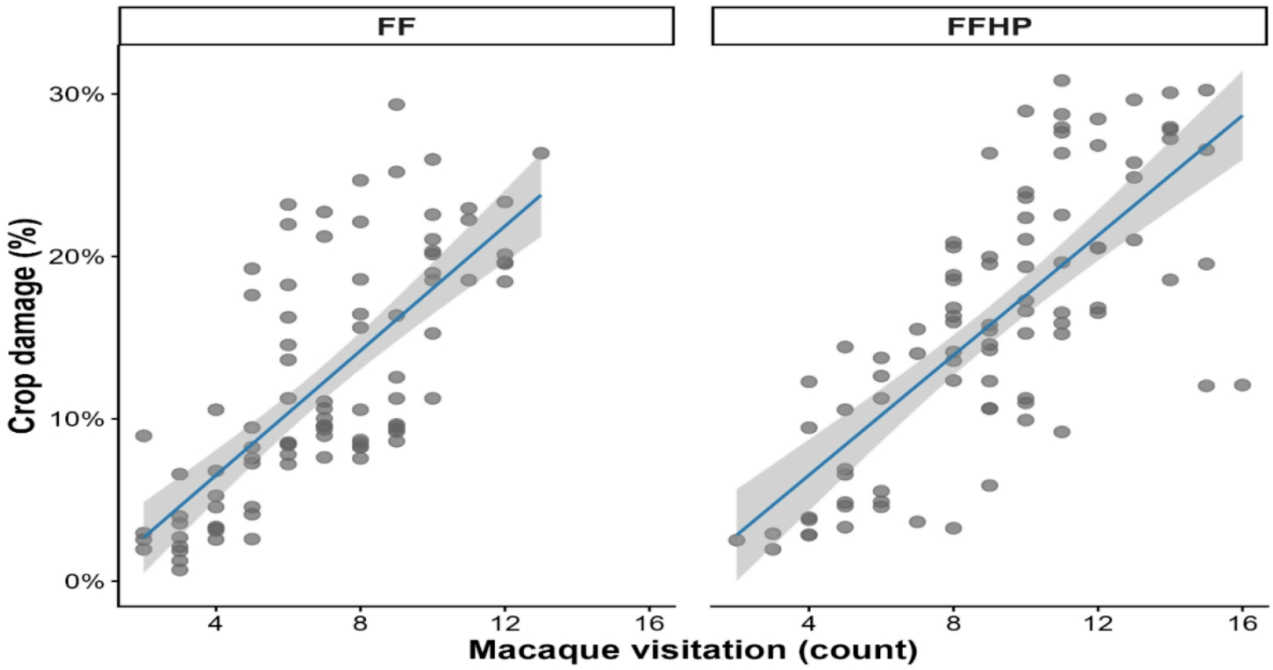


Figure 4

Relationship between macaque visitation (count) and crop damage (%) across forest fringe (FF) and forest fringe with human population (FFHP) habitats. Each point represents an observation (treatment × season × location; n = 6 locations per habitat). Solid lines represent linear regression fits with 95% confidence intervals. Spearman's rank correlation indicated strong positive relationships in both habitats (FF: rs = 0.75; FFHP: rs = 0.73; $p < 0.001$).